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MASSIVE DEVONIAN RUGOSA OF BELGIUM

JAMES E. SORAUF

[State University of New York at Binghamton, Binghamton, New York]

ABSTRACT

The massive colonial rugose corals are an important segment of the fossil faunas of the Givetian and Frasnian rocks of Belgium. The term massive embraces all colonies in which corallites are in lateral contact, with or without intercorallite walls. The type of construction of intercorallite wall varies between the two families encountered, the Disphyllidae and the Phillipsastraeidae. Colonial forms are referred to as cerioid if the intercorallite wall has a layer of epitheca (e.g., in Disphyllidae) and pseudocerioid if the wall is non-epithecal (e.g., in Phillipsastraeidae). Septal fine structure is equally valuable, in phillipsastraeids characterized by septal trabeculae diverging near the inner margin of the dissepimentarium (trabecular fans) and in disphyllids by septal trabeculae bending progressively inward as the dissepimentarium is traversed from intercorallite wall to tabularium. Specialized dissepiments are developed in the Belgian phillipsastraeids in the innermost dissepimentarium, but not to the extreme degree and uniformity noted in the horseshoe dissepiments of some genera of the family.

All massive Belgian species belonging to the family Phillipsastraeidae have been placed in *Phillipsastraea*. Two types of development are noted within the genus, one tending toward forms characterized by specialized dissepiments and spindle-shaped septal dilation, and the other toward smaller corallites with no specialization of dissepiments, but with a well-developed, compact wall around the tabularium. This inner wall results from extreme and localized dilation of septal trabeculae. The species of *Philipsastraea* studied are *P. hennahi*, *P. goldfussi*, *P. pentagona*, and *P. macrommata*.

All massive species properly placed in the family Disphyllidae are included in the genus *Hexagonaria*. These are *H. hexagona*, *H. quadrigemina*, *H. davidsoni*, *H. philomena*, *H. rohrensis*, *H. darwini*, and *H. hypocrateriformis*.

In addition to descriptions of the Belgian forms of these species descriptive material is presented for the type specimens of *Phillipsastraea hennahi*, *Hexagonaria hexagona*, and *H. quadrigemina*. Where sufficient data have been available, scatter diagrams are of use in outlining the amount of variability encountered in the Belgian species. The diagrams herein plot the mean number of septa for each colony versus the mean diameter of the tabularium, rather than corallite diameter.

INTRODUCTION

This study was inaugurated during a year (1960-61) spent in Belgium at the University of Louvain in the laboratory of paleontology under the supervision of Professor MARIUS LECOMPTE. During this term, it was decided to evaluate the morphology and taxonomy of the massive Devonian rugose corals, principally from the standard sections of stages of Middle and Upper Devonian Series in the Dinant Basin. As a secondary consideration, the identification was undertaken of massive corals from these stages represented in the collections of the Royal Museum of Natural History in Brussels.

During the term spent in Belgium at the University of Louvain, I had access to all thin sections of massive Devonian corals in collections at both the University and the Royal Museum. Many additional thin sections were prepared by the technical staffs of both university and museum, and more have been prepared in the Department of Geology of the State University of New York at Binghamton.

In the fall of 1963, I was able to visit the British Museum (Natural History) in London, the Museum of Natural History in Paris, the Senckenberg Museum in Frankfort, and the University of Bonn, to study type specimens and thin sections of collections described by SMITH, MILNE-EDWARDS & HAIME, GOLDFUSS, and others.

ACKNOWLEDGMENTS

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STRATIGRAPHY AND STRATIGRAPHIC PALEONTOLOGY

STRATIGRAPHY

The importance of the Middle and Upper Devonian sedimentary rocks of southern Belgium and neighboring France to stratigraphers is considerable, as shown by the number of stages with type areas in the Dinant Basin (Fig. 1).

Type Devonian Areas of Dinant Basin

Upper Devonian	Fammenian—Les Fammenes, Belgium
	Frasnian—Frasnes, Belgium
Middle Devonian	Givetian—Givet, France
	Couvinian—Couvin, Belgium

The rocks themselves are a complex of platform carbonates and shales, and basinal shales. The platform carbonates include not only lagoonal and open marine limestones, but important biohermal and biostromal carbonates as well. Work by LECOMPTE in the past 30 years has led to an understanding of detailed stratigraphic correlations and changing bathymetric and ecological conditions in the Devonian shelf seas of the Dinant and Namur basins.

The following is a resumé of salient features of Givetian and Frasnian stratigraphy, intended to form a framework for consideration of the coral faunas described below.

The Givetian rocks of the Dinant Basin have been subdivided into four units, referred to by letters *a* through *d*, as summarized below (ref. *19*, p. 84-85).

Givetian Rocks of Dinant Basin

Gi_d Uppermost, biostromal, marked by massive stromatoporoids, massive tabulate corals (*Alveolites, Thamnopora*), and *Hexagonaria quadrigemina*.

Gi_c Well-bedded limestones, fauna of solitary rugose corals, gastropods, and *Spinocyrtia mediotextus*.

Gi_b Biostromal in large part, fauna of *Stringocephalus burtini*, tabulate and solitary rugose corals, and abundant stromatoporoids.

Gi_a Basal, argillaceous limestones thin (approx. 3 m.), bearing *Emanuella undifera* and solitary corals.

This basic stratigraphic sequence does not vary greatly within the Dinant Basin, although as Givetian units are traced from south to north, biostromal units (Gi_b and Gi_d) are replaced by impure limestones and all units thin markedly (*19*, p. 12, fig. 2). Approximately 425 m. of Givetian

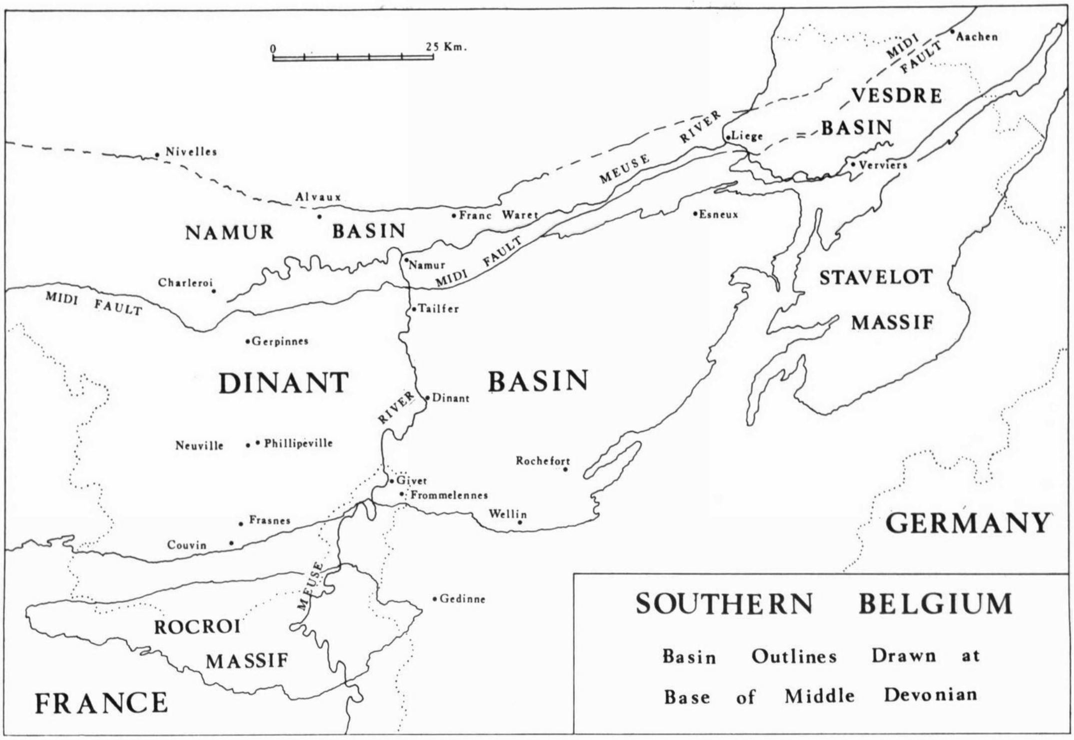

FIG. 1. Sketch map of souuthern Belgium showing localities mentioned in text. Basin outlines taken from geologic map of Belgium (1954).

strata at Couvin (and more at Givet) at the south flank of the Dinant Basin is equivalent to considerably less than 100 m. at Tailfer at the north edge of the same basin. In the Namur Basin, thickness of Givetian rocks varies from 30 to 70 m. (*5*, p. 139), where the beds are referred to as the Assise d'Alvaux.

The Frasnian of the Dinant Basin is divided into three large units, from the base, Assise de Fromelennes (F_1), Assise de Frasnes (F_2), and Assise de Matagne (F_3). Lower and middle Frasnian units are generally further divided, employing a letter system to indicate position.

Lower Frasnian beds (F_1) are in large part argillaceous limestones, especially at the base and top. At Fromelennes, the middle part of the sequence (F_{1b}) is biostromal in large part, with abundant stromatoporoids and tabulate corals (*22*, p. 92), while basal and upper (F_{1a}, F_{1c}) beds are more argillaceous and nodular, presenting evidence of a subsiding basin floor. As F_1 strata are traced to the north flank of the Dinant Basin, the unit thins, and becomes highly argillaceous, and as traced into the Namur Basin, remains argillaceous, with shales and impure limestones present. The most probable equivalent of the F_1 at the north flank of the Namur Basin is the Assise of Mazy (*18*, p. 336), a unit of reddish, calcitic shales and sandy limestones.

Middle Frasnian (F_2) rocks show considerable complexity, which has been deciphered in large part by LECOMPTE in the Dinant Basin as the result of detailed study of the strata, their inferred bathymetric conditions of deposition, and correlation on the basis of changes in these conditions. On the south flank of the Dinant Basin, in the area of Frasnes, the subdivisions of the Frasnian and characteristic development is as follows (condensed from LECOMPTE, 1956, 1958, 1960, and VAN WINKEL, 1964):

Frasnian Divisions in Southern Dinant Basin

Top of Middle Frasnian

F_{2j} Bioherms of red limestones with rich faunas of *Phillipsastraea* (formerly referred to as "*Acervularia*"), with some tabulate corals and sparse brachiopods.

F_{2i} Shales, calcareous shales, and thin-bedded limestones with fauna rich in brachiopods and corals in lower part. Less fossiliferous above, surrounds F_{2j} bioherms.

F_{2h} Biohermal accumulations of reefal limestones, largely built by stromatoporoids with talus levels of clastic limestone.

F_{2g} Bedded limestones, form base for growth of F_{2h} bioherms.

F_{2f} Gray shales, seen only in areas without bioherms in F_{2d}.

F_{2e} Green shales, seen only in areas without bioherms in F_{2d}.

F_{2d} Bioherms built largely of tabulate corals in lower part and massive stromatoporoids in the upper part.

F_{2c} Argillaceous limestone and calcareous shale passing laterally into limestones forming base for F_{2d} bioherms.

F_{2b} Argillaceous, nodular limestones with *Cyrtospirifer bisinus*.

F_{2a} Shales and nodular limestones with *Cyrtospirifer orbelianus* (so-called *"zone des monstres"* of J. GOSSELET).

This total sequence has a composite thickness of approximately 500 m. on the southern margin of the Dinant Basin. As the middle Frasnian is traced northward in the Dinant Basin, several trends are evident. The first of these is a marked decrease in thickness and percentage of shale. The middle Frasnian is only 100 m. thick at Tailfer at the northern end of the Dinant Basin (*44*, p. 3), where only the F_{2a-b} division contains a shale unit. At Aisemont, on the south flank of the Namur Basin, thickness is reduced still further to approximately 80 m. with thin shale units present in the F_{2a-b} and F_{2e-f} divisions (*44*, pl. 14).

The most striking change in facies seen as middle Frasnian beds are correlated northward is noted in the carbonate units. Each of the biohermal units can be equated to biostromes. F_{2d} and F_{2h} bioherms are replaced by stromatoporoid biostromes at the position of Neuville and Phillippville (Fig. 1) in the central Dinant Basin. The F_{2j} bioherms are replaced by a biostrome farther north, at Gerpinnes and Tailfer in the northern Dinant Basin, and throughout the Namur Basin (*44*, p. 112).

The upper Frasnian (F_3) is represented by the Schistes de Matagne in the Dinant Basin and by the shaly Assise de Franc-Waret in the Namur Basin. This unit marks the final phase of Frasnian sedimentation, accompanying downwarping of the Basin floor ending formation of reefoid and associated carbonates.

STRATIGRAPHIC PALEONTOLOGY

Devonian rocks in Belgium known to contain massive rugose corals are limited to the Givetian and Frasnian Stages.

The Givetian coral fauna is characterized by an abundance of colonies of *Hexagonaria quadrigemina*. In the Dinant Basin, all subdivisions of the Givetian above the Gi_a contain this species. The shaly Gi_a beds most probably represent an unfavorable biotope, as no colonial corals are noted in these beds. Above, the Gi_b and Gi_d units of the typical sequence at Givet both contain *H. quadrigemina*. The species is most abundant in the basal Gi_d beds beneath the stromatoporoid biostromes comprising the bulk of the unit.

Other species noted in Givetian rocks are *Hexagonaria hypocrateriformis* and *H. rohrensis* (both from Gi_b of southern Dinant Basin), although each seems to be extremely limited in abundance.

In the overlying Frasnian rocks, no massive colonial corals are noted below the first occurrence of *Hexagonaria hexagona* in F_{2g} beds of the southern Dinant Basin. This species is very abundant in the uppermost and lateral portions of the F_{2h} bioherms and in the lower 5 or 6 m. of the overlying F_{2i} shales of the southern Dinant Basin. In this part of the basin, *H. hexagona* is extremely abundant, seemingly to the exclusion of other species. In the Namur Basin however, *H. hexagona* occurs at several levels throughout the middle and upper portions of the middle Frasnian (F_2), where it is sporadically accompanied by *H. davidsoni*, *H. philomena*, and *H. darwini*. None of these occurrences have been seen in the field by me, but rather are noted on specimen identification cards in the Musée Royale d'Histoire Naturelle in Brussels.

The *Phillipsastraea* fauna is highly characteristic of the overlying middle Frasnian rocks of the Dinant Basin. The red F_{2j} bioherms contain very abundant specimens of this species, referred to commonly as *"Acervularia."* Within the bioherms themselves have been collected *P. pentagona*, *P. goldfussi*, and *P. macrommata*. From the F_{2i} immediately underlying or lateral to the bioherms, or both, have been collected very abundant *P. hennahi*, *P. pentagona*, *P. pentagona minima*, *P. goldfussi*, and *P. macrommata*. *P. goldfussi* and *P. pentagona* are well represented in upper middle Frasnian (F_{2III}) rocks of the Namur Basin.

MORPHOLOGY OF CORALS

Only systematic descriptions based on a sound understanding of morphological features of Rugosa can be meaningful. In massive colonial forms, a number of such features can be significant—colonial form, fine structures of walls and septa, configuration of dissepiments and tabulae (and dissepimentaria and tabularia), relative importance and appearance of radial (septa) and horizontal (dissepiments and tabulae) elements in construction of the coral exoskeleton, and lastly, the development of specialized skeletal features. Of these, it is rare that any one single structure forms a valid basis for taxonomic differentiation. However, some structures must be regarded as more closely related to the morphology and manner of growth of the rugose polyp, and thus assume greater importance. For the families treated in this study, the configuration of trabeculae within septa and walls is highly important in classification as shown by the work of Wang (1950) and Rozkowska (1953).

COLONIAL FORM

The term massive colonial Rugosa is here used as a general term to include all colonial forms in which individual corallites are in lateral contact with their neighbors. Within this grouping are recognized: 1) cerioid colonies, in which an epithecal wall is present between corallites; 2) pseudocerioid colonies (see glossary) in which a nonepithecal wall separates the corallites; and 3) plocoid colonies, in which no continuous wall is present between adjacent corallites united by septa and dissepimental tissue.

The question of multiform occurrences of species or genera is puzzling. It seems possible and probable that under certain ecologic conditions, fasciculate (loosely bundled) colonies can and do form massive colonies, and vice versa. To date, no well-documented evidence is available to prove or disprove this hypothesis in the case of Devonian genera. However, change from pseudocerioid to partially plocoid colonial forms can be demonstrated. A single species may show stages of gradation between forms with nonepithecal walls present throughout the corallum, forms with such walls partially present, and forms essentially without walls, truly plocoid. Pseudocerioid colonies were most frequently noted in bioherms, where all individuals of certain species (e.g., *Phillipsastraea goldfussi, P. pentagona*) are pseudocerioid. In argillaceous rocks, many colonies are plocoid. It thus seems that some ecologic control over colonial form exists.

WALL STRUCTURE

Previously noted is the fact that many massive Devonian corals have walls between the corallites. Where the walls are of an epithecal nature, the colonies are here called cerioid and where walls are not epithecal, the colonies are here called pseudocerioid. I propose the latter term because of what I consider a basic difference between the two types, both morphologic and taxonomic. If cerioid is employed (as currently) for all massive colonies with walls between corallites, then both *Phillipsastraea* and *Hexagonaria* have species with cerioid forms. However, it is the manner of wall formation which differs markedly between the genera, and the families to which they belong. *Hexagonaria* is characterized by a three-layered intercorallite wall, while *Phillipsastraea* displays a single-layered wall that is septal in construction and in aspect.

The three-layered wall of cerioid forms of the Disphyllidae contains a central layer of fine-grained calcite which appears as a dark line in transverse sections (Fig. 2). This is regarded as being the equivalent of the epitheca of solitary corals. Glinska (1955, p. 81) referred to this as the *"Grenzstreif,"* and assigned considerable taxonomic weight to its path as seen in transverse sections of *Hexagonaria.* I prefer to call this layer the epitheca, following usage of Rozkowska (1960, p. 9) and Schouppé (1958, p. 233). The dark coloration of the layer is most likely due to the very fine grain size of the constituent calcite. Wise & Hay *(45)* have concluded that dark coloration of centers of trabeculae in Recent Scleractinia is due to the form and small size of constituent crystals rather than organic or inorganic residues of opaque material. This conclusion appears applicable to the epitheca of the Rugosa also.

Rozkowska (*28,* p. 9) referred to the layers of fibrous calcite lying on both sides of the epitheca as pseudotheca, "either consisting of thickened

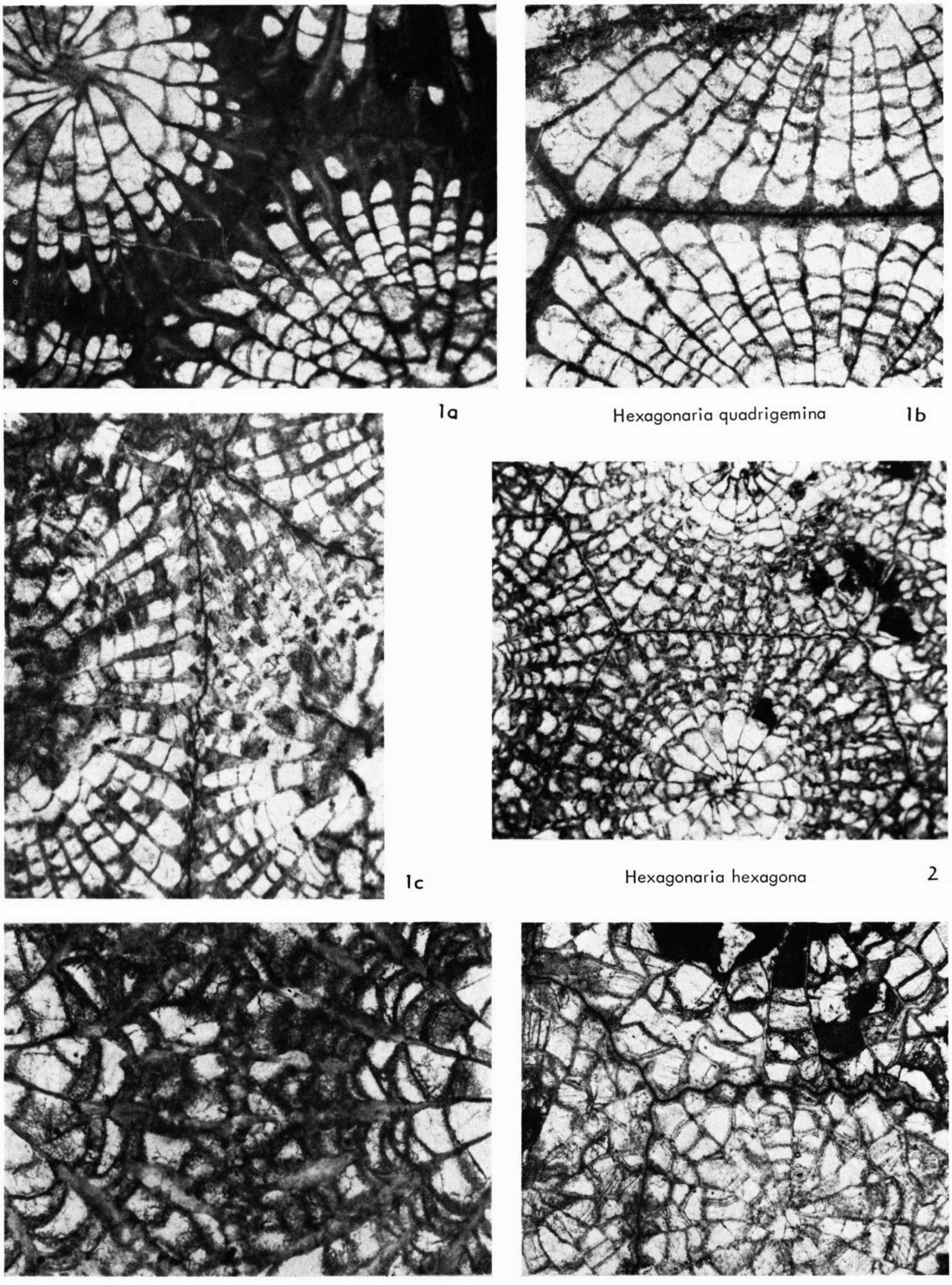

Fig. 2. Wall structure of *Hexagonaria* and *Phillipsastraea* shown by transverse sections (all $\times 10$ except as indicated otherwise).

distal ends of septa (septotheca) connected by laminate stereozone, or of thick-walled dissepiments (paratheca)." I do not employ the terms pseudotheca, septotheca, or paratheca in respect to the fibrous layers of the intercorallite wall, since it seems improper to use Scleractinian terminology for nonanalogous structures in Rugosa. This terminology should be reserved for structures arising independently of the epithecal wall.

Thickness of the epithecal walls to a certain degree is characteristic of groups of species within *Hexagonaria*. Species such as *H. quadrigemina* and *H. hypocrateriformis* typically have thick, straight walls. The thick fibrous layers are the result of coalesced, heavy-based, attenuate septa, generally in an opposition position to septa of neighboring corallites (Fig. 2,*1a-c*). Septa are numerous enough to line the intercorallite wall space of the corallite more or less. Thinner-walled *Hexagonaria* are much more variable in wall path, many with corallite walls displaying a zigzag path in transverse sections as an expression of septal furrows. Where septa are in an offset position to those of adjacent corallites, the development of septal furrows follows naturally (Fig. 2,*4*). It should be noted that this feature is most common in species such as *H. hexagona* that have narrow septal bases and septal dilation at the border of the tabularium. While presence or absence of an epithecal wall is useful in separating Disphyllidae from Phillipsastraeidae, the thickness and straightness of walls is only a general index to groups within the genus *Hexagonaria*.

Individuals within species of *Phillipsastraea* have a markedly different type of intercorallite wall, lacking epitheca and similar or identical in construction to septa (Fig. 2,*3*). This has been referred to as pseudothecal by Rozkowska (1960, p. 9) and Schouppé (1958, p. 233), both of whom employ wall structure to differentiate between cerioid Disphyllidae and (pseudocerioid) Phillipsastraeidae. I refer to such intercorallite walls as nonepithecal. It is this septal construction which appears to be largely responsible for a progressive loss of walls within a single species. Such a series can be seen in *P. hennahi*, where the walls consist of vertical rows of trabeculae, and are seemingly identical in construction to distal ends of the septa. For this reason fragmented wall segments seem to be "captured" and incorporated as septal extensions in plocoid forms.

SEPTAL FINE STRUCTURE

Trabeculate construction of the septa is considered as primary in importance for differentiation of massive genera belonging to the Disphyllidae and the Phillipsastraeidae. *Hexagonaria* of the Disphyllidae is characterized by a trabecular structure in septa consisting of parallel trabeculae attached at the epithecal wall, and sloping upward and inward toward the axis of the corallite (Fig. 3,*1a,e*; 4,*2c*). *Phillipsastraea* (Phillipsastraeidae) is characterized by fans of trabeculae, with the trabeculae sloping upward obliquely from an area of divergence paralleling the outer margin of the tabularium, and located near its outer margin (Fig. 3,*2*; 5,*2*). This, in conjunction with related morphological features, is used for differentiation between these family-groups.

The above is something of an oversimplification. Variations in these two plans do exist, and

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Fig. 2. *(Explanation continued from facing page.)*

1. Hexagonaria quadrigemina (Goldfuss), Middle Devonian (Givetian).——*1a,* Specimen from unit Gi_b at loc. 7999, Marche sheet, Belgium, (MRHNB no. 11692) with thick epithecal walls and spindle-shaped distal portions of septa.——*1b,c*. Specimen from unit Gi_d at Mont d'Haurs, Givet, France (Sorauf coll., USNM) showing *(1b)* extremely straight epithecal wall and septa in opposition and *(1c)* clearly defined epithecal layer in intercorallite wall which undulates slightly where septa are offset; *1b* and *1c* from same corallum.

2. Hexagonaria hexagona (Goldfuss), Upper Devonian (Frasnian), from lower part of unit F_{2i} in Lion Quarry, Frasnes, Belgium (Sorauf coll., USNM) showing epithecal wall with straight path where septa of adjoining corallites are opposed but undulating in right-hand part of section.

3. Phillipsastraea goldfussi (de Verneuil & Haime), Upper Devonian (Frasnian), from upper F_{2i} at Beauchateaux Quarry, Senzeille, Belgium (Sorauf coll., USNM), showing nonepithecal wall seen without any central epitheca, apparently identical to outer part of septa, ×19.5

4. Hexagonaria philomena Glinski from F_{2IIb} at loc. 6339F, Mettet sheet, Belgium (MRHNB no. 16364), showing epithecal wall with undulating path and short "groins" (infolds) of epitheca in distal end of septa, ×12,

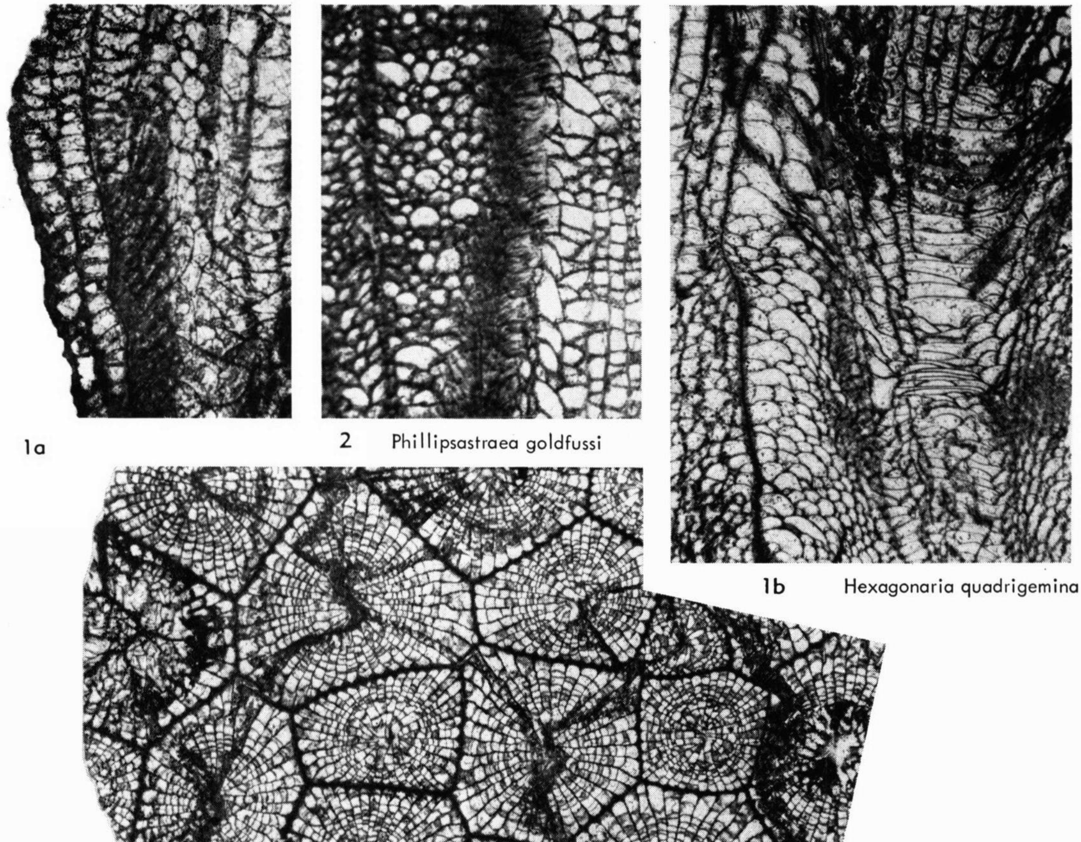


FIG. 3. *Hexagonaria* and *Phillipsastraea* from Middle and Upper Devonian of Belgium and France.

1. *Hexagonaria quadrigemina* (GOLDFUSS), Middle Devonian (Givetian).——*1a.* Specimen from unit Gi_{IIIc} at loc. 9340, Spy sheet, Belgium (MRHNB no. 12893) longitudinal section showing very well-preserved septal trabeculae in outer dissepimentarium, ×9.——*1b-d.* Specimen from basal part of unit Gi_d from Mont d'Haurs, Givet, France, illustrating most typical development of this species

can cause confusion. Certain of the disphyllids do show a tendency toward reflexing of the peripheral calicinal platform, leading to the presence of a rim around the calicinal pit and associated tendency toward spreading of septal trabeculae. *Billingsastraea* (Disphyllidae) shows this spreading, as illustrated by STUMM (1953, pl. 1) and STRUZ (1965, p. 524). No specimens of *Hexagonaria* studied show this tendency.

It must be emphasized that compact fans of trabeculae are generally associated with specialization of dissepiments and characteristic of spindle-like dilation of septa in the phillipsastraeids. Thus differentiation between the genera and families studied can be made on a firm basis.

SEPTAL DILATION AND FORMATION OF INNER WALL

In advanced species of *Hexagonaria* such as *H. hexagona,* and in many species of *Phillipsastraea,* septa are strongly dilated at the border of the tabularium. In *Hexagonaria,* such dilation is never more than two to three times the minimum thickness of the septa, and the number of septa (32 to 40) is not large compared to the circumference of the tabularium. As a result, it is rare that the spaces between septa are small enough that Belgian forms have an inner wall, however poorly developed. An outstanding example of a species in which deposition of secondary calcite has led to the presence of such a wall is *Hexagonaria laxa,* figured by ROZKOWSKA (1960, p. 14). Even in such an extreme case as this, I am hesitant to use the terms theca or pseudotheca, since no other structures are present to suggest that a functional analogy to the scleractinian theca existed.

In *Phillipsastraea,* both first- and second-order septa may be strongly dilated near the border of the tabularium, as in *P. hennahi.* This dilation, referred to as "spindle-shaped," is characteristic of the genus and results from lateral expansion and divergence of trabeculae as seen in transverse sections. As a result of this dilation of septa, accompanied by deposition of secondary calcite on smaller, arched, specialized dissepiments, an inner wall is formed surrounding the tabularium.

In several species of *Phillipsastraea* (e.g., *P. pentagona, P. goldfussi*) a remarkable development of a compact inner wall is noted at the border of the tabularium, forming a solid sheath which separates it from the dissepimentarium. Here the septa remain uniformly thin from the distal end to the point where they are markedly dilated to form the wall. As shown in Figure 6 the inner wall is formed by vertical rows of expanded trabeculae, one row representing each of the septa and joined laterally to neighboring septa to form a compact wall of calcite. The wall, as developed in some individuals bears a marked physical resemblance to the septotheca of the Scleractinia.

In some colonies in which the compact inner wall is developed, major septa do not extend into the tabularium. Within *Phillipsastraea pentagona* can be found individuals with little or no septal dilation, some with weak spindle-shaped dilation, and others with strong, localized dilation to form a compact inner wall (Fig. 6,*1a-e*). It is also of interest to note here that colonies displaying the thin, compact wall tend not to develop any specialization of dissepiments and trabecular divergence within septa is negligible (Fig. 7).

CARINAE

In *Phillipsastraea,* intergrades can be observed between noncarinate and weakly carinate forms. Weak carinae, when present, are most commonly

FIG. 3. *(Explanation continued from facing page.)*

as seen in Dinant Basin, longitudinal section *(1b)* showing numerous globose dissepiments and fairly complete flat tabulae, ×3, transverse sections *(1c,d)* illustrating numerous attenuate septa reaching to axis of corallite and quadripartite budding well shown in corallite at left margin of *1c* associated with other corallites exhibiting fourfold septal patterns prior to their breakup into fours, specimen *(1d)* illustrating corallites with smaller size than average but with approximately same septal counts, ×2.——*1e.* Longitudinal section of specimen from unit Gi_{IIIc} from loc. 1, Spy sheet, Belgium (MRHNB no. 12948) showing large angle between trabeculae and epithecal wall characteristic of the species, ×9.

2. *Phillipsastraea goldfussi* (DE VERNEUIL & HAIME), Upper Devonian (Frasnian), from unit F_{2i} at Beauchateaux Quarry, Senzeille, Belgium (Sorauf coll., USNM), longitudinal section showing tight fans of septal trabeculae, ×11.5.

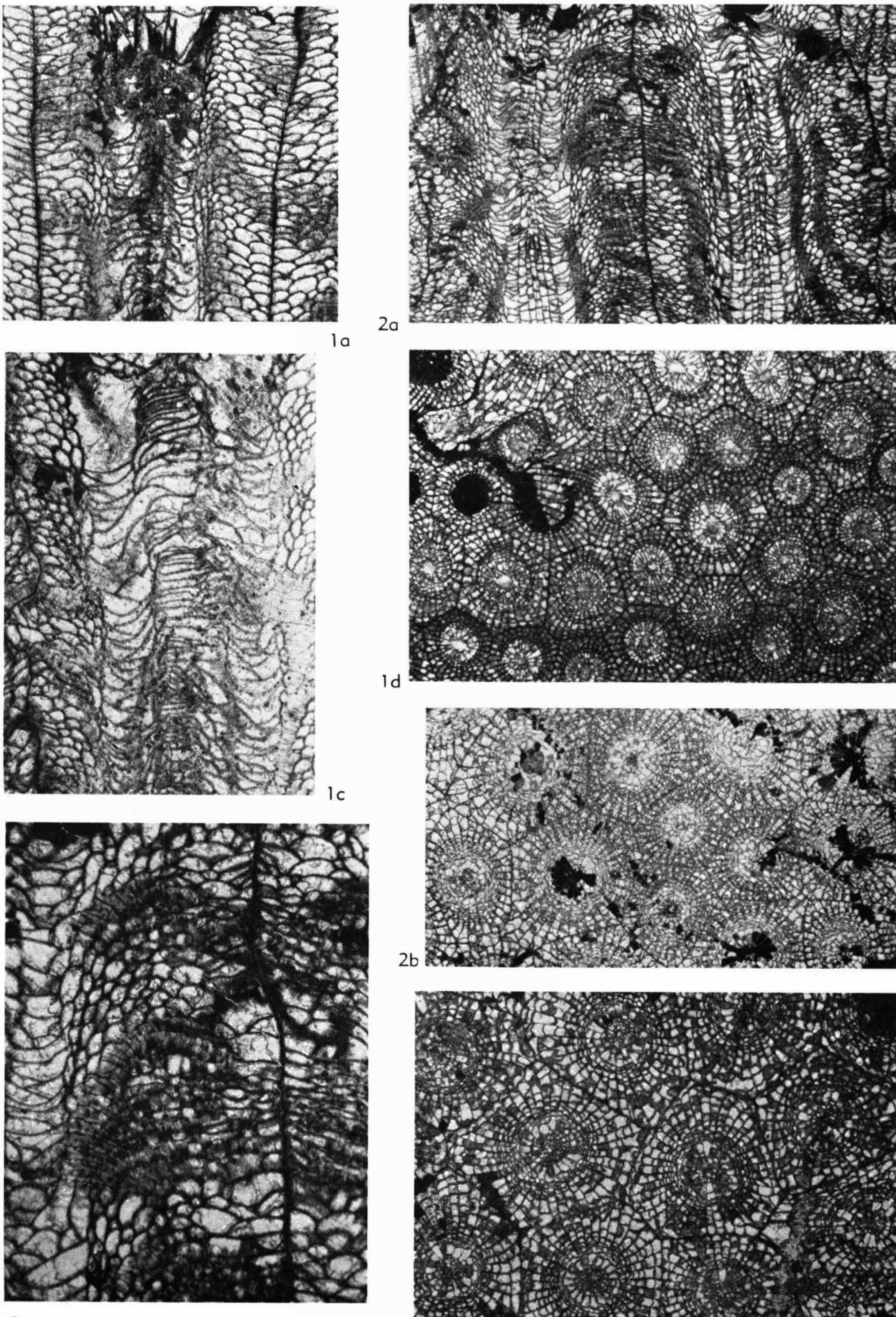


FIG. 4. Septal and dissepimental structures of *Hexagonaria hexagona* (GOLDFUSS), Upper Devonian (Frasnian), of Belgium.

expressed as knobby lumps within septa seen in transverse sections. Within the *P. hennahi* species group, when septa are weakly carinate, so are the intercorallite walls. In all members of the genus, carinae result from swollen trabeculae present at intervals within septa and wall. In longitudinal view, trabecular fans are seen to be composed of more loosely bundled, swollen trabeculae (Fig. 8,*1c,d*).

In *Hexagonaria,* carinae are only weakly developed in the Belgian fauna. In a majority of specimens showing weak zigzag carinae, they appear as little more than spinose projections, caused by meandering septa joining dissepimental tissue with a small amount of secondary calcite deposited at the junction.

The presence or absence of weak, knobby, zigzag carinae in *Hexagonaria* and *Phillipsastraea* is not here regarded as of taxonomic significance. Both weakly carinate and noncarinate corallites may be present within the same colony in both genera. However, no individuals of either genus were present in the fauna with strong cross-bar carinae (yard-arm). It would be incorrect to imply that these specialized septal structures are also of nontaxonomic value.

DISSEPIMENTS

The following discussion is divided into two parts, the first dealing with the presence or absence of specialized dissepiments and their taxonomic value, and a second discussing variations in the size and number of dissepiments within a single species.

Numerous workers have underscored the presence of specialized dissepiments, especially horseshoe dissepiments, and have used the presence or absence of them as the basis for taxonomic differentiation of genera, subfamilies, or families. Schouppé (1958) argued for differentiation of genera on the basis of the presence or absence of horseshoe dissepiments, and thus regarded *Billingsastraea* as being a *Phillipsastraea* without horseshoe dissepiments (p. 237). This decision was made after discovering horseshoe dissepiments in the corallum of the type specimen of *P. hennahi*. As stated below, *Billingsastraea* has other basic differences and cannot be regarded as being closely related to *Phillipsastraea*. It should be noted, however, that many corallites in the type specimen of *P. hennahi* do *not* show development of horseshoe dissepiments.

Soshkina (1954, p. 65) erected the "group" Thamnophyllida for forms having septal trabecular fans and horseshoe dissepiments, with the single family Thamnophyllidae within the group. Rozkowska (1956, p. 261) discussed the grouping within the order Phillipsastraeacea, all characterized by the presence of trabecular fans within the septa. She separated these forms into families in large part upon the presence or absence of horseshoe dissepiments.

In the present study of the phillipsastraeids of Belgium, it has been found that the presence or absence of specialized dissepiments themselves cannot be utilized as a single definitive characteristic, even at the species level. Individual corallites of *Phillipsastraea hennahi* display a marked variation in the perfection of formation of the specialized rows of arched dissepiments along the line of trabecular divergence in the septa (Fig. 5, 7,*4,* 8,*1*). In spite of this variation, I judge that the *tendency* toward formation of specialized dissepiments is very important. It appears that formation of such dissepiments is closely allied to the uparching of the basal plate of the polyps resulting in the formation of 1) fans of trabeculae

Fig. 4. *(Explanation continued frof facing page.)*

1. Specimens from basal part of unit F_{2i} at North Quarry, Frasnes (Sorauf coll., USNM).——*1a,b.* Longitudinal and transverse sections of corallum with little septal dilation and typical development of axial and periaxial series of tabulae, ×4, ×2.——*1c,d.* Longitudinal and transverse sections of corallum illustrating form common in some colonies with narrow tabularium and showing epithecal nature of intercorallite wall as well as excellent development of tabulae in axial and periaxial series, ×5, ×2.

2. Specimens from unit F_{2i} at Lion Quarry (Sorauf coll., USNM).——*2a,b.* Longitudinal and transverse sections of typical colony showing trabeculae progressively inclined inward and characteristic number of septa with dilation near border of tabularium, ×3, ×2.——*2c.* Longitudinal section of specimen with excellently preserved septal trabeculae subparallel to epithecal wall in outer dissepimentarium, progressively inclined toward tabularium in inner dissepimentarium, ×9.

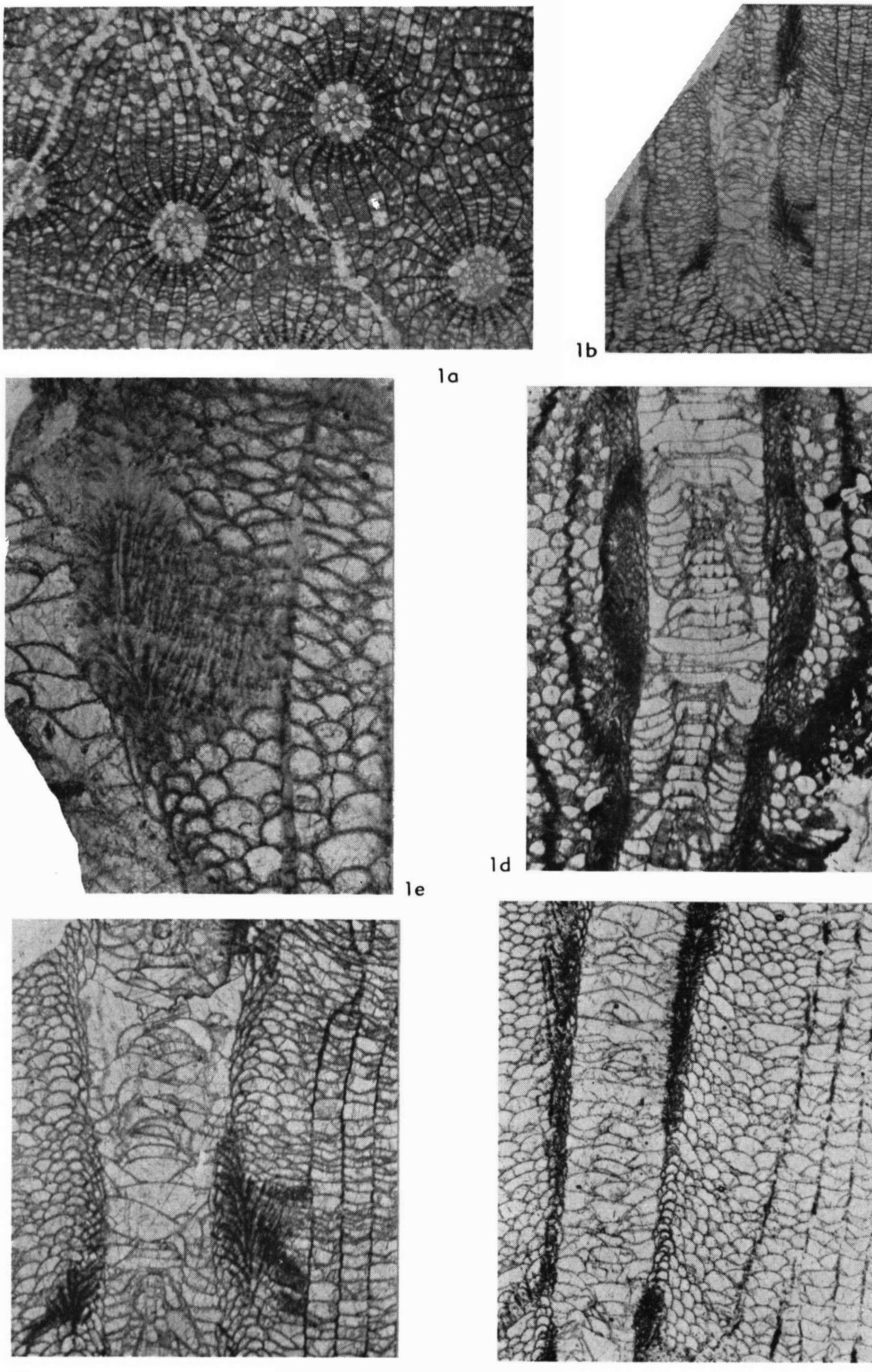


FIG. 5. *Phillipsastraea hennahi* (LONSDALE), Upper Devonian (Frasnian), from unit F_{2i}, Belgium.

within the septa with the line of divergence close to the outer margin of the tabularium, and 2) the formation of an inner wall surrounding the tabularium. All individuals belonging to the *Phillipsastraea* genus group demonstrate this tendency (i.e., toward arching in the dissepiments to more or less parallel the arching of the basal plate indicated by the fans of divergent trabeculae in the septa). The tighter and more symmetrical the fan of septal trabeculae becomes, the greater the tendency toward development of one or more rows of uparched dissepiments in the position under the area of trabecular divergence. The end result of this tendency is the presence of a single row of greatly uparched horseshoe dissepiments, like those of *Thamnophyllum* or *Macgeea*. The question then arises as to the validity of *Pachyphyllum* (MILNE-EDWARDS & HAIME). The present study did not uncover specimens attributable to *Pachyphyllum*. However, in *Phillipsastraea* no forms were seen with consistent development of the single uniform row of horseshoe dissepiments characteristic of species of *Pachyphyllum*. Although artificial, the most useful method of distinguishing between the two groups is to continue to regard species with consistent development of a single row of uniform horseshoe dissepiments as belonging to *Pachyphyllum*. Species belonging to *Pachyphyllum* can be easily differentiated from those belonging to *Phillipsastraea*. The latter genus appears to occupy a somewhat less specialized position evolutionarily, with individuals displaying greater plasticity in almost all features than does *Pachyphyllum*, which almost certainly is an evolutionary offshoot from *Phillipsastraea*, thus containing features in common.

Another point of interest as to the development of dissepiments in *Phillipsastraea* is variation of the number of rows of dissepiments in their individual size. Figure 5 also illustrates the great variation present—from 3 to 5 rows of almost hemispherical dissepiments, to 9 or 10 rows of greatly flattened dissepiments in individuals with comparable width of dissepimentaria. This is a feature which has been employed at times in defining species. Differences in size of dissepiments are in general a reflection of differences in rate of growth, most probably as a result of genetic or ecologic factors. J. W. WELLS (personal communication, 1965) stated that such variation is common in the scleractinians, and that the size and number of dissepiments can be noted to vary greatly among individuals belonging to the same species and living within a few feet of each other on the sea floor. It seems that the number and size of dissepiments are a reflection of rate of enlargement of the calyx, but that variations of number and size are not always due to genetic or environmental factors, but may simply reflect differences between individual colonies.

TABULARIUM

Various types of tabularia and tabular configurations are present within the genera *Hexagonaria* and *Phillipsastraea*.

Hexagonaria is divisible into two groups of species in the Belgian fauna. The first to appear is the *H. quadrigemina* group which is characterized by relatively wide tabularium and narrow dissepimentarium, as well as the tendency toward development of septa that are attenuate or shortened. This group is characterized by long, stout tabulae which characteristically are somewhat flat-topped, and are generally complete, with only minor tabellae present at the lateral margins of the tabularia. A more advanced, somewhat later group within the genus is typified by *H. hexa-*

FIG. 5. *(Explanation continued from facing page.)*

1. Specimens from Senzeille sheet, Belgium.——*1a-c.* Transverse and longitudinal sections of specimen from loc. 6146 (MRHNB no. 15696) similar to type with moderate dilation of septa and intercorallite walls generally present, differing in that no specialized dissepiments are developed, longitudinal section showing open trabecular fan and irregular axial and periaxial tabulae, ×3, ×3, ×6.——*1d.* Longitudinal section of specimen from loc. 7132 (MRHNB no. 15959) with tight fans of septal trabeculae, arched specialized dissepiments in area of divergence, and regular axial and periaxial tabulae, ×6.——*1e.* Longitudinal section of specimen from Beauchateaux Quarry (Sorauf coll., USNM), showing open fan of septal trabeculae, ×19.5.

2. Longitudinal section of specimen from Neuville Quarry, Neuville (Sorauf coll., USNM), with tight fans of septal trabeculae, numerous small unspecialized dissepiments, and irregular axial and periaxial tabulae, ×5.

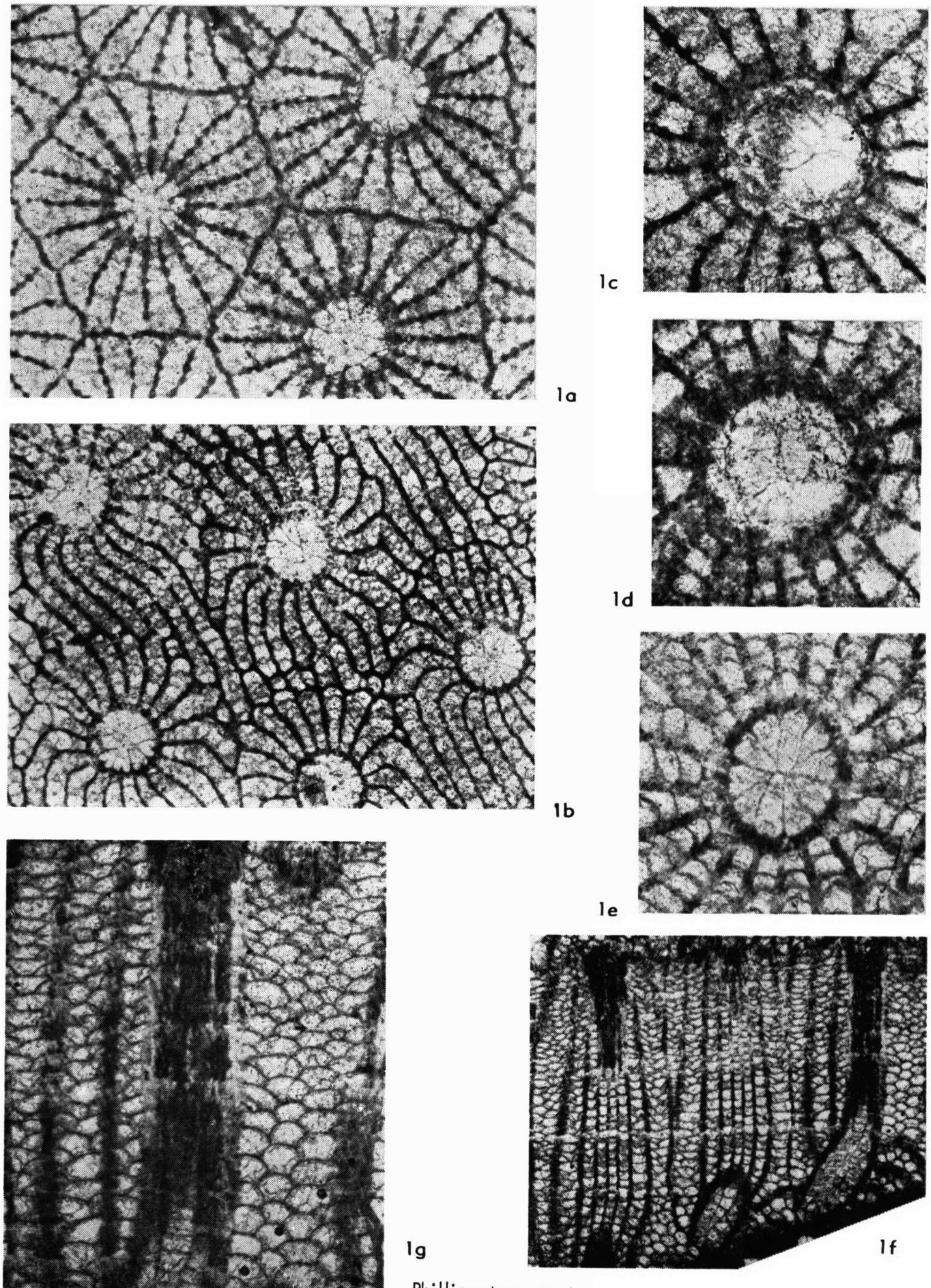


FIG. 6. Sections of *Phillipastraea pentagona* (GOLDFUSS) frof Upper Devonian) (Frasnian) of Belgium illustrating formation of inner wall of corallites.

1a,b. Transverse sections of specimens from unit F_{2i} at Neuville Quarry, Neuville, *(1a)* (Sorauf coll., USNM) lacking wall around tabularium and *(1b,* MRHNB no. 15686) with compact inner wall surrounding tabularium, both $\times 12$.

gona, with relatively broader dissepimentarium, septa dilated at the border of the tabularium, and with major septa reaching to or almost to the axis of the corallite. This group of species is characterized by the differentiation of axial and periaxial tabulae, the axial series forming flat-topped domes, and periaxial tabulae appearing in longitudinal sections as leaning against the walls of the tabularium and sagging somewhat. The configurations of tabulae, and their completeness is considered in large part to be a result of the interference of septa with the floor of the calicinal pit (formed by the tabulae). Long-septate species show axial and periaxial series of tabulae, while forms with shorter septa have the tendency toward development of more complete tabulae in the broader, flat-bottomed calcinal pit.

Some species of *Phillipsastraea* are characterized by long septa, joining at the axis of the corallites, and these also have tabulae that are differentiated into axial series of flat-topped domes and sagging periaxial tabular plates. In *P. hennahi* however, great variability in this feature can be seen (Fig. 5,*1c,3*; 7,*4*). As a result of this variability, configuration of tabulae (by itself) is considered untrustworthy for taxonomic purposes within *Phillipsastraea,* except in a broad way.

It is of interest to note here that, within the species, *Phillipsastraea pentagona,* forms that develop a compact, thin inner wall were at the same time characterized by a straight-walled, flat-bottomed calycinal pit. In these coralla, tabulae are uniformly complete, only slightly arched or sagged, and with a minimum number of accessory plates present.

GLOSSARY

The reader is referred to the excellent glossary of terms applicable to Scleractinia, Tabulata, and Rugosa in Volume F, Coelenterata, of the *Treatise on Invertebrate Paleontology* (Moore, ed., 1956). The following includes only terms which postdate the *Treatise* volume, or which are actually or possibly employed here in a somewhat different sense than that given in the *Treatise.*

area of divergence. Area in phillipsastraeids seen in longitudinal sections as line of divergence of septal trabeculae, causing fanlike configuration of trabeculae; invariably found in inner dissepimentarium.

cerioid. Colonial form in which prismatic neighboring corallites are separated by 3-layered wall, middle layer of which is analogous to epitheca of solitary, dendroid, or phacelloid corals. (*See* pseudocerioid.)

epitheca. In cerioid colonial corals, thin layer of dark, fine-grained calcite forming central part of intercorallite wall.

epithecal wall. Intercorallite walls in cerioid colonial corals with central layer of epitheca.

fine structure (septal). Structures of septa (trabeculae, etc.) which may be discerned with low-power microscope (Kato, 1963). These were referred to as microstructure by Wang (1948) and Rozkowska (1952).

horseshoe dissepiments. Specialized dissepiments found in some corals with septal trabeculae in fans. Horseshoe dissepiments are invariably developed in area of divergence of septal trabeculae. This term should only be used for highly specialized dissepiments which show their greatest width somewhere above the base, and which occur in a single, uniform row. (*See* specialized dissepiments.)

inner wall. Wall formed at boundary of tabularium and dissepimentarium, or in axial portion of dissepimentarium. Inner wall is formed by lateral expansion of septa alone, or by such expansion accompanied by thickening of dissepiments bordering tabularium.

nonepithecal. Intercorallite walls found in some massive colonial corals in which central epithecal layer is absent, not as result of recrystallization. Nonepithecal wall is similar or identical to outer portions of septa in construction. This type of wall has been referred to by Rozkowska (1953, 1965) and Schouppé (1958) as pseudotheca. (*See* pseudocerioid).

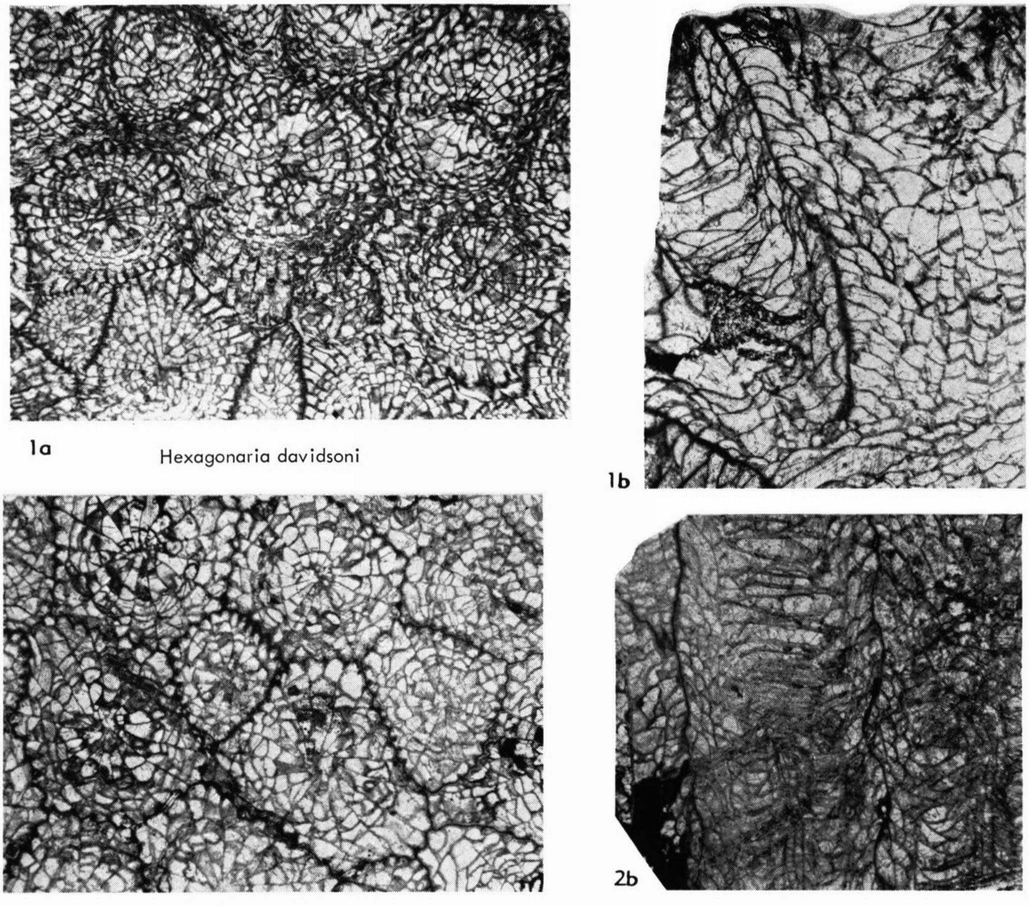
pseudocerioid. Colonial form of massive corals with nonepithecal intercorallite walls that are formed of single layer of calcite, and are similar or identical in construction to outer portions of septa. (*See* cerioid; nonepithecal.)

specialized dissepiments. Any dissepiments which are consistently smaller, larger, or more globose than others in dissepimentarium. Specialized dissepiments are commonly found in area at or near outer margin of tabularium (in area of divergence of septal trabeculae in Phillipsastraeidae). Horseshoe dissepiments are

Fig. 6. *(Explanation continued from facing page.)*

1c-e. Transverse sections of central part of corallites from unit F_{2j} at Neuville Quarry *(1c,d)* and unit F_{2i} at Beauchateaux Quarry, Senzeille (both Sorauf coll., USNM), showing essentially undilated septa *(1c),* moderately dilated septa *(1d),* and very localized strong dilation of septa forming inner wall *(1e),* all ×19.5.

1f,g. Longitudinal section of specimen from unit F_{2i} at Beauchateaux Quarry (Sorauf coll., USNM), showing inner wall composed of parallel trabeculae, in places seen in section tangential to wall, ×9, ×20.



1a Hexagonaria davidsoni

1b

2a Hexagonaria philomena

2b

3 Hexagonaria hypocrateriformis

4 Phillipsastraea hennahi

Fig. 7. Sections of *Hexagonaria* and *Phillipsastraea* from Middle Devonian (Givetian) and Upper Devonian (Frasnian) of Belgium.

an extreme form of specialized dissepiments and not actually seen in any corals mentioned herein.

trabecular fans . Configuration of septal trabeculae such that when viewed in longitudinal sections trabeculae appear to form fans either symmetrical or asymmetrical to line of divergence paralleling margin of tabularium.

CLASSIFICATION

REVIEW OF FAMILY-GROUP CLASSIFICATION

In recent years, a number of workers have studied colonial Devonian corals and several have proposed systems of classification reaching upward at least to the family-group level. It is significant that there is no real agreement between these, as they have been based on differing philosophies, and each author has chosen different morphological features as the main basis of classification. Several broad areas of agreement exist, and these will be examined. The following section deals only with the families Disphyllidae and Phillipsastraeidae, and only taxa of the family-group level are discussed here. Generic classification is considered in greater detail in the following section of this paper.

STUMM (1949) in his study of the Devonian tetracorals proposed the following classification:

Classification of Tetracorals by Stumm (1949)

FAMILY	SUBFAMILY	GENERA (among others)
Disphyllidae	Disphyllinae (without aulos or horseshoe dissepiments)	*Hexagonaria* *Billingsastraea* *Phillipsastraea*
	Pachyphyllinae (with horseshoe dissepiments)	*Pachyphyllum* *Macgeea* *Phacellophyllum* *Thamnophyllum*
	Eridophyllinae (with aulos)	

This early classification by STUMM disregarded two factors that I consider of primary importance. He did not consider the fine structures of the septa in his classification, and as a result placed *Phillipsastraea* (with septal trabeculae in diverging fans) in the same subfamily as *Hexagonaria* and *Billingsastraea* (which have a parallel, inclined configuration of septal trabeculae); or the tendency for *Philipsastraea* to develop specialized dissepiments in the area of divergence. The most extreme form of this specialization is the presence of horseshoe dissepiments, but the trend is apparent in many individuals which cannot properly be said to have true horseshoe dissepiments.

WANG (1950, p. 217) defined the family Disphyllidae as containing solitary and colonial corals with a well-developed dissepimentarium and one or more fan systems of septal trabeculae, with divisions as follows:

Classification of Disphyllidae by Wang (1950)

FAMILY	SUBFAMILY	GENERA (among others)
Disphyllidae	Disphyllinae (septa without trabecular divergence)	*Disphyllum* *Cyathophyllum* *Hexagonaria*
	Phacellophyllinae (septa with trabecular divergence)	*Phillipsastraea* *Thamnophyllum* *Macgeea*

WANG did not discuss the presence or absence of horseshoe dissepiments within the family, and

FIG. 7. *(Explanation continued from facing page.)*

1. *Hexagonaria davidsoni* (MILNE-EDWARDS & HAIME) from unit F_{2IIc} of Frasnian at loc. 6338, Walcourt sheet (MRHNB no. 16433), transverse section *(1a)* showing typically large number of attenuate septa, ×3, and longitudinal section *(1b)* illustrating flat complete tabulae with accessory plates near dissepimentarium composed of few rows of dissepiments, ×5.
2. *Hexagonaria philomena* GLINSKI from same unit and locality as *1* (MRHNB no. 16434), transverse section *(2a)* showing small number of attenuate septa, short second-order septa, and zigzag path of epithecal wall, ×3, and longitudinal section *(2b)* showing axial and periaxial series of tabulae at lower left, ×5.
3. *Hexagonaria hypocrateriformis* (GOLDFUSS) from unit G_{IIa} of Givetian at loc. 14b, Tamines sheet (MRHNB no. 13042), transverse section showing typical large tabularium, many attenuate septa, and open axial area, ×2.
4. *Phillipsastraea hennahi* (LONSDALE) from unit F_{2i} of Frasnian at loc. 6797, Senzeille sheet (MRHNB no. 15531), longitudinal section showing open fans of coarse septal trabeculae, specialized dissepiments, and uniform axial and periaxial tabulae, ×6.

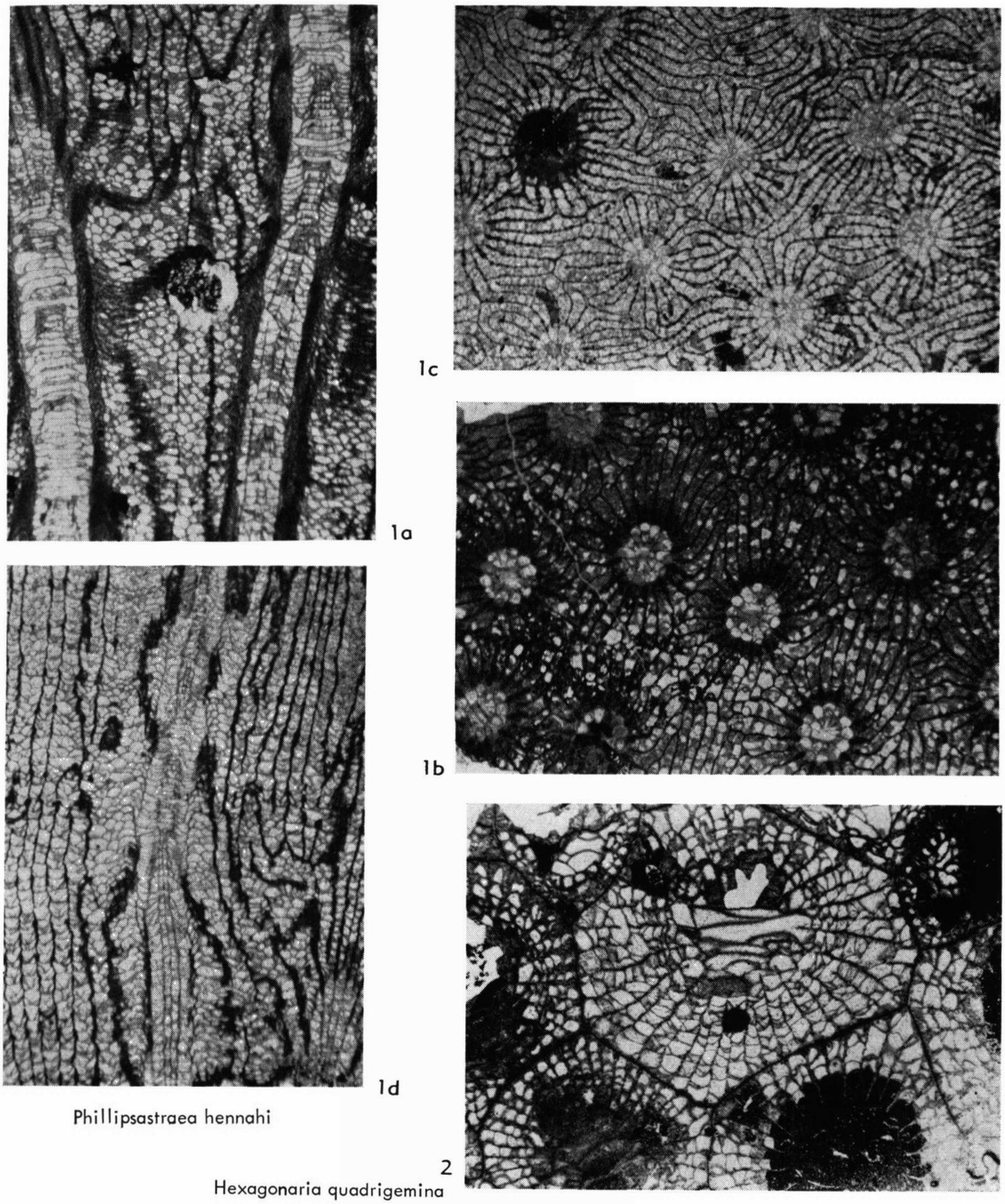


FIG. 8. *Phillipsastraea* from Upper Devonian (Frasnian) and *Hexagonaria* from Middle Devonian (Givetian) of Belgium.

1. *Phillipsastraea hennahi* (LONSDALE) from Frasnian unit F_{2i}.——*1a,b*. Longitudinal and transverse sections of corallum from loc. 7132, Senzeille sheet, (MRHNB no. 15959) with well marked septal dilation and some secondary calcite forming inner wall around tabularium, and well-developed specialized dissepiments, both ×3.——*1c,d*. Transverse and longitudinal sections of specimen from loc. 6797, Sautour sheet (MRHNB no. 15531) with weak knobby carinae, very little septal dilation, and intercorallite walls partially lacking, both ×3.

2. *Hexagonaria quadrigemina* (GOLDFUSS) from Givetian unit Gi_{IIIc} at loc. 1, Spy sheet (MRHNB no. 12948), transverse section showing septa not reaching axis but rather with open space in tabularium typical of many coralla, ×3.

it must be assumed that he considered such specialized dissepiments closely related to trabecular divergence in the septa. WANG's groups at the subfamily level are approximately the same as my families.

E. D. SOSHKINA, beginning in 1939, published important works on Devonian Rugosa from the Ural Mountains and the Russian Platform (1939, 1949, 1951, 1954). SOSHKINA (1939, p. 7) early stated her basic premise that the configuration of tabulae and dissepiments should be features of greatest systematic importance, with character of septa (including structural types) of second greatest importance. In later papers she regarded ontogeny and form of budding as of equal status to factors listed above. SOSHKINA presented a system of classification in 1939 *(34)* and modified it somewhat later *(35-37)*. The following groups include genera which I place in the Disphyllidae and Phillipsastraeidae.

Familial Placement of Genera by Soshkina (1939)

FAMILY	GENERA (among others)
Thamnophyllidae (parricidal budding, hexacoralloid features)	*Thamnophyllum* *Macgeea* *Pachyphyllum*
Neocampophyllidae (colonial, nonparricidal budding, axial differentiation in tabularium, etc.)	*Schlueteria* *Phillipsastraea*
Peneckiellidae (plano-convex tabulae, nonparricidal budding, etc.)	*Peneckiella* *Keriophylloidea* *Megaphyllum* *Tabellaephyllum* *Donia*

SOSHKINA's generic taxa present numerous difficulties, summarized here as an aid in evaluating her families. The genus *Phillipsastraea,* as defined by SOSHKINA, is based on *"P. radiata"* (MARTIN) SMITH (1917, p. 298), previously noted that this species is Carboniferous in age and may possess a columnella, and placed it in the genus *Orionastraea.* It is evident that SOSHKINA's interpretation of *Phillipsastraea* includes forms assignable to the genera *Hexagonaria* and *Phillipsastraea* (based on *P. hennahi*). The genus *Megaphyllum,* and possibly also *Donia* are composed of species more properly assignable to *Hexagonaria,* including *Megaphyllum hexagonum* (*36,* p. 21, 36). Since *P. hennahi* was placed in the genus *Pachyphyllum* by SOSHKINA, the latter, as defined by her, includes many forms assignable to *Phillipsastraea.*

SOSHKINA's family groupings are unsatisfactory. The family Neocampophyllidae (name not available, no nominate genus) includes species with divergent fans of septal trabeculae and species with parallel septal trabeculae. In my opinion, this family grouping only serves to mask true relationships, and genera should be placed in two families, one with divergent trabeculate fans and associated structures, and the other without these features. The family Peneckiellidae is based on the genus *Peneckiella.* BULVANKER (1958, p. 178) pointed out that *Peneckiella* has horseshoe dissepiments at the outer border of the tabularium, and should be placed in the Thamnophyllidae of SOSHKINA. The presence of trabeculate fans and horseshoe dissepiments in the type species, *Peneckiella minor* as illustrated by SCHOUPPÉ (1958, p. 230) and HILL (1956, p. 283), underscores the correctness of this opinion. The Thamnophyllidae of SOSHKINA is thought to include a closely-related group of genera, although I would not consider parricidal budding diagnostic as she did. The family does include *Phillipsastraea hennahi* (labeled *Pachyphyllum hennahi* by SOSHKINA, 1951, p. 84) and thus should be referred to as the Phillipsastraeidae.

In 1962, SOSHKINA *(38),* and in part SOSHKINA & DOBROLYUBOVA *(38),* modified considerably the previous classification of SOSHKINA. Their listing of pertinent families and genera is as follows:

Classification of Massive Devonian Rugose Corals by Soshkina & Dobrolyubova (1962)

FAMILY	GENERA
Thamnophyllidae (horseshoe dissepiments, septal costae above epithecal sheath, septal trabeculae in fans)	*Thamnophyllum* *Pachyphyllum* *Macgeea*
Disphyllidae (all colonial, deep calicinal pit, tabulae rarely complete)	*Disphyllum* *Hexagonaria* *Peneckiella* *Donia*
Phillipsastraeidae (all colonial, deep calicinal pit, rim sometimes around tabularium, tabulae commonly differentiated)	*Phillipsastraea* *Billingsastraea* *Eridophyllum*

SOSHKINA did not change the family Thamnophyllidae, but did change its taxonomic position, placing it in the order Cystiphyllida. She erected a new order of exclusively colonial corals, the Evenkiellida, which contains the Disphyllidae and Phillipsastraeidae. The Disphyllidae, at this date treated as the senior synonym of Peneckiellidae SOSHKINA, contains phacelloid and cerioid colonial genera. Of these, *Hexagonaria* was now regarded as based on the type species *Cyathophyllum hexagonum* GOLDFUSS. In addition, the genus *Megaphyllum* SOSHKINA, 1939, was placed in synonymy with *Hexagonaria*. The family Phillipsastraeidae replaced the Neocolumnariidae SOSHKINA, 1949, to include three genera. *Phillipsastraea* was here regarded as based on the type *Astraea hennahi* LONSDALE, rather than *A. radiata* MARTIN.

Although an improvement over previous classifications of SOSHKINA, this also presents several difficulties. The genus *Phillipsastraea*, with basic similarities to species included in SOSHKINA's family Thamnophyllidae, was placed in a different order, in spite of identical septal construction and specialization of dissepiments. The order Evankiellida also appears unnecessary, as the only real unifying factor of the group is the colonial nature of the included genera.

M. ROZKOWSKA (1953) adopted the family-group taxa proposed by WANG, because of their basis on the fine structure of septa and walls.

Classification of Disphyllidae by Rozkowska (1953)

FAMILY	SUBFAMILY	GENERA (among others)
Disphyllidae	Pachyphyllinae (trabeculae in fans and with horseshoe dissepiments)	*Pachyphyllum* *Thamnophyllum* *Macgeea*
	Disphyllinae (no horseshoe dissepiments in single genus studied)	*Phillipsastraea*

WANG's (1950) subfamily Phacellophyllinae was replaced by the name Pachyphyllinae, and the basis for classification altered somewhat. Whereas WANG placed all forms with septal trabeculae in fans in the subfamily Phacellophyllinae, ROZKOWSKA placed corals with trabecular fans but without horseshoe dissepiments in the subfamily Disphyllinae. ROZKOWSKA later (1957, p. 83) altered this system, following SOSHKINA in placing genera previously considered as Pachyphyllinae in the Thamnophyllidae, and erected the subfamilies Thamnophyllinae (colonial forms) and Macgeeinae (solitary corals) within the family.

ROZKOWSKA (1965) has recently clarified and expanded her classification of the family groups containing corals with septal trabeculae in the fan configuration, all of which she placed in the suborder Phillipsastracea.

Three families are placed as follows:

Classification of Phillipsastracea by Rozkowska (1965)

FAMILY	GENERA
Macgeeidae (with epitheca and horseshoe dissepiments, mostly solitary)	*Macgeea*, and others
Phillipsastraeidae (without epitheca, and with or without horseshoe dissepiments, all colonial)	*Phillipsastraea*, and others
Marisastridae (with epitheca, but without horseshoe dissepiments)	*Marisastrum*, possibly also *Ceratophyllum*

The genus *Marisastrum* ROZKOWSKA, 1965, is based on the type species *Cyathophyllum sedgwicki* EDWARDS & HAIME, reported from Frasnian rocks of Belgium. No corals have been noted in this study with truly cerioid walls (with epitheca) and fanlike configuration of septal trabeculae. I would combine Macgeeidae and Phillipsastraeidae into one family bearing the latter name.

HILL (1956) put the massive species under consideration in the family Phillipsastraeidae C. F. ROEMER, 1833, as follows:

Classification of Phillipsastraeidae by Hill (1956)

FAMILY	SUBFAMILY	GENERA (among others)
Phillipsastraeidae	Phillipsastraeinae (no aulos or well-defined horseshoe dissepiments)	*Phillipsastraea* *Disphyllum* *Hexagoniaria* *Billingsastraea*
	Phacellophyllinae (no aulos, but with well-defined horseshoe dissepiments)	*Phacellophyllum* *Thamnophyllum* *Peneckiella* *Macgeea* *Pachyphyllum*

HILL placed the family Disphyllidae HILL, 1939, in synonymy with the Phillipsastraeidae. The Phillipsastraeinae is the subfamily including forms without aulos or horseshoe dissepiments. I would modify this grouping by placing all genera without aulos but with septal trabeculae in the fan-shaped configuration in the same group. Thus, *Phillipsastraea* is shifted from the group with *Disphyllum, Hexagonaria,* and *Billingsastraea* to the latter grouping of HILL, her subfamily Phacellophyllinae, which may be regarded as a family-group with nominate genus *Phillipsastraea.* The remainder of HILL's first subfamily then displays the parallel trabecular structure in septa and an absence of such features as the pronounced calicinal rim or horseshoe dissepiments. This group should be based on the nominate genus *Disphyllum* and referred to the Disphyllidae of HILL, 1939.

SCHOUPPÉ (1959, p. 217), placed all forms characterized by a centrally located area of divergence of septal trabecular in the suborder Phillipsastraeacea. Within the suborder, SCHOUPPÉ stated that horseshoe dissepiments are always developed in solitary and phacelloid forms, but only sporadically found in plocoid colonies. His classification follows:

Classification of Phillipsastraeacea by Schouppé (1958)

FAMILY	SUBFAMILY	GENERA
Macgeeidae	Macgeeinae (horseshoe dissepiments, accompanied by a peripheral zone of horizontal dissepiments)	*Macgeea (Macgeea)* *Macgeea (Thamnophyllum)* *Trapezophyllum*
	Peneckiellinae (horseshoe dissepiments, but no horizontal, peripheral dissepiments)	*Peneckiella*
Phillipsastraeidae (with and without horseshoe dissepiments, with trabecular fans)		*Phillipsastraea* *Billingsastraea*

The effectiveness of this classification is greatly lessened by a misconception regarding the generic characteristics of *Billingsastraea.* Material from North America which must be congeneric with *B. verneuili* indicates that this genus is not closely related to *Phillipsastraea.* I would unite all of the genera listed by SCHOUPPÉ in the family Phillipsastraeidae. He did not study any species referable to the genus *Hexagonaria.*

BULVANKER (1958) followed essentially the same system of classification as proposed by SOSHKINA in her previous works. The portions of the BULVANKER classification pertinent to the present study are as follows:

Classification of Massive Rugosa by Bulvanker (1958)

FAMILY	GENERA
Thamnophyllidae	*Thamnophyllum* *Macgeea*
Phillipsastraeidae	*Pachyphyllum* *Phillipsastraea* *Columnaria* *Schlueteria*
Hexagonariidae	*Hexagonaria* *Megaphyllum* *Tabellaephyllum* *Donia*

The family Thamnophyllidae was retained as employed by SOSHKINA, the sole change being the placement of species belonging to the genus *Peneckiella* with horseshoe dissepiments in the family Thamnophyllidae, presumably (but not stated) as belonging in the genus *Thamnophyllum.* The family Phillipsastraeidae, BULVANKER, proposed by her in the form of a new combination, must be rejected. BULVANKER (1958, p. 118) followed SOSHKINA (1951, p. 95) in selecting *"Phillipsastraea" radiata* (MARTIN) as type species of the genus. From this choice has arisen a false concept of the genus and thus of the family. BULVANKER has included in the genus many species with true epithecal wall and parallel configuration of septal trabeculae. These should be placed in *Hexagonaria.* Mixing of genera with parallel construction of septal trabeculae (as in *Columnaria*) and fan-shaped configuration (as in some species placed by BULVANKER in *Phillipsastraea*) in the same family clouds a basic morphological difference.

The family Hexagonariidae was proposed by BULVANKER as a substitution for Peneckiellidae SOSHKINA 1949, as *Peneckiella* was placed in the

Thamnophyllidae by BULVANKER. This family-group is also rejected for several reasons. First, family characteristics which are based on *Hexagonaria* must be identical to the characteristics of the family Disphyllidae HILL, 1939, as the fasciculate genus *Disphyllum* closely resembles in all ways but form of colonial growth the cerioid genus *Hexagonaria*. Second, this family grouping is founded on an erroneous choice of type species for the genus, leading to the exclusion of species, including *H. hexagona* (GOLDFUSS), characterized by dilated septa at the outer margin of the tabularium. The choice of *Cyathophyllum hexagonum* as genolectotype for *Hexagonaria* by LANG, SMITH, & THOMAS (1940, p. 69) has priority and has been unchallenged to this date. As previously stated, the genera *Megaphyllum* and *Donia* are regarded by me as junior subjective synonyms of *Hexagonaria*.

FAMILY AND GENUS GROUPS

I am employing the following family-group taxa to include, *among others*, the genera listed. (1) Family Phillipsastraeidae ROEMER 1883: *Phillipsastraea, Pachyphyllum, Thamnophyllum, Peneckiella, Macgeea.* (2) Family Disphyllidae HILL 1939: *Disphyllum, Hexagonaria, Billingsastraea.*

Distinguishing characteristics of these two families and of the genera *Hexagonaria, Phillipsastraea,* and *Billingsastraea* are described in this section of the paper, followed by descriptions of species of *Phillipsastraea* and *Hexagonaria* in the section on "Systematic Paleontology."

Family PHILLIPSASTRAEIDAE Roemer

Phillipsastraeidae C. F. ROEMER, 1883, p. 389;——*(partim)* HILL, 1956, p. 279;——*(partim)* SCHOUPPÉ, 1958, p. 232;——*(partim)* SOSHKINA & DOBROLYUBOVA, 1962, p. 336.
Thamnophyllidae SOSHKINA, 1949, p. 76;——SOSHKINA & DOBROLYUBOVA, 1962, p. 308.
Peneckiellidae *(partim)* SOSHKINA, 1949, p. 141.
Pachphyllinae STUMM, 1949, p. 35;——ROZKOWSKA, 1953, p. 12.
Phacellophyllinae WANG, 1950, p. 219.
Disphyllinae *(partim)* ROZKOWSKA, 1953, p. 57.
Neocampophyllidae *(partim)* SOSHKINA, 1954, p. 44.
Macgeeidae SCHOUPPÉ, 1958, p. 218.

Diagnosis.—Solitary, phacelloid, pseudocerioid, and plocoid corals unified by following characteristics: all genera with septal trabeculae arranged in system of divergent fans, with area of divergence positioned at or near border between tabularium and dissepimentarium. This trabeculate configuration is closely related to 1) tendency toward development of specialized dissepiments in area of divergence, trending toward appearance of true horseshoe dissepiments in its most extreme form, and 2) development of raised rim surrounding central calicinal pit. In highly advanced genera of family these characteristics are expressed as calicinal prominence coinciding with single row of uniform horseshoe dissepiments. Solitary and phacelloid genera have septal ridges above their external sheath of epitheca.

Remarks.—The unifying characteristics of the family enumerated above are those called "hexacoralloid" by SOSHKINA (1951) in reference to the family Thamnophyllidae SOSHKINA. In my opinion, the classification of SOSHKINA is based too heavily on features of the calyx and tabularium, features which appear to me to be too variable to be employed as generic characteristics.

The characteristics of the Phillipsastraeidae are best expressed by the group that has commonly been referred to the subfamily Pachyphyllinae (or Phacellophyllinae). Descriptions of these groups have been too restricted by reliance on the presence or absence of horseshoe dissepiments however. I include in the genus all forms that display a tendency toward formation of specialized dissepiments around the tabularium.

Genus PHILLIPSASTRAEA d'Orbigny

Phillipsastraea D'ORBIGNY, 1849, p. 12;——SMITH, 1917, p. 284;——LANG, SMITH, & THOMAS, 1940, p. 99;——STUMM, 1949, p. 34;——*(partim)* WANG, 1950, p. 220;——*(partim)* SOSHKINA, 1951, p. 95;——ROZKOWSKA, 1953, p. 57;——HILL, 1956, p. 280;——SCHOUPPÉ, 1958, p. 235;——*(partim)* BULVANKER, 1958, p. 118;——SOSHINA & DOBROLYUBOVA, 1962, p. 336.
Pseudoacervularia ROZKOWSKA, 1953, p. 49.
Billingsastraea (partim) SCHOUPPÉ, 1958, p. 237.
Pachyphyllum (partim) BULVANKER, 1958, p. 89.

Diagnosis.—Composed of pseudoceriod or plocoid corals characterized by septal trabeculae in fans. Septa always of two orders, with first-order septa ordinarily extending well into tabularium, commonly with some bilateral symmetry observable especially so when septa join at axis. In species with long first-order septa, axial and periaxial series of tabulae are developed. In species with shorter septa, tabulae are commonly complete and deflected in either oral or aboral direction. Tendency within genus toward development of specialized dissepiments near border of tabularium. In some individuals, these dissepiments approach configuration of true horseshoe form. Outer, unspecialized dissepiments are small, uniform, and numerous. Some septa are carinate, but never bear carinae of yard-arm type. Budding nonparricidal. Intercorallite walls when present are septal in construction and lack an epithecal layer.

Remarks.—D'ORBIGNY (1849, p. 12) introduced the name *Phillipsastraea,* listing two examples, *Astrea parallela* and *A. hennahi* (*32*, p. 285). In 1850, MILNE-EDWARDS & HAIME listed the type species of *Phillipsastraea* as *Astraea hennahi* LONSDALE (p. lxvi) (Devonian). However, in 1851, by placing *Astraea hennahi* as type species of their new genus *Smithia*, and later choosing the Carboniferous species *Erismatolithus radiatus* MARTIN, 1809, as type species of the genus *Phillipsastraea* (1853, p. 203), they restricted the genus improperly to forms exclusive of the type species.

The valid fixation of the types species of *Phillipsastraea* by MILNE-EDWARDS & HAIME in 1850 has priority over any other subsequent designation (Zool. Code, 1961, art. 69,a) and is not susceptible of being changed.

SMITH (1917) thoroughly discussed usage of the name *Phillipsastraea*, confirmed the propriety of employing *P. hennahi* as type for the genus, and chose a lectotype specimen for the species. Since that date, all paleontologists have regarded the genus as based on the type species *P. hennahi,* with two notable exceptions—SOSHKINA (1951, 1954) and BULVANKER (1958). This is not to imply that workers dealing with the genus have always paid proper attention to descriptions by SMITH, or to features of the lectotype. On the contrary, numerous misconceptions have arisen regarding the genus, as a result of inadequate knowledge of the type specimen and a lack of knowledge regarding the morphology of, and variation within the species as a whole.

SMITH (1945) made several important points. He stated that "corallites are united by their dissepimental tissue or are separated by thin, degenerate epitheca," and that "the dissepiments forming the wall of the tabularium are often smaller and more globose than the rest, corresponding to the horseshoe dissepiments of *Disphyllum (Phacellophyllum), Macgeea*, and other allied genera" (1945, p. 36, 37). He also stated that horseshoe dissepiments are very well developed in many species of the genus (1945, p. 37). It is not possible to evaluate the meaning of this last statement, because *Pachyphyllum* was regarded by SMITH as a synonym of *Phillipsastraea.* SMITH also placed some pseudoceriod species of *Phillipsastraea* in the genus *Prismatophyllum* (now *Hexagonaria*). An example of this is *Prismatophyllum schucherti* SMITH (1945, p. 48).

STUMM (1949) regarded *Phillipsastraea* as a plocoid disphyllid coral genus, separated from *Billingsastraea* by the presence of septal dilation at the border of the tabularium, and stratigraphically by its occurrence in Upper Devonian rocks, as *Billingsastraea* is restricted to Middle Devonian strata. Both genera, along with *Hexagonaria* were placed in the subfamily Disphyllinae by STUMM. In my opinion, *Phillipsastraea* is not closely related to the other two genera.

WANG (1950) regarded *Phillipsastraea* as containing plocoid coralla with septal trabeculae deviating from the septal plane, with a marked area of divergence of the trabeculae. WANG did not mention specifically the presence or absence of horseshoe dissepiments, but did include the genus *Pachyphyllum* as a junior synonym.

Distribution.—Phillipsastraea is widespread in upper Frasnian rocks of western Europe and makes an excellent stratigraphic indicator of Frasnian age in England, NE. France, Belgium, Germany, Spain, Poland, Russia, and western North America (U.S. and Canada).

The genus is also reported from Middle and Upper Devonian rocks of Australia (HILL, 1936), Lower Devonian rocks of Australia *(12),* and from Middle Devonian strata of China (*1,* p. 122). The genus is reported from one locality in Germany (Brilon, Enkelberg) in Fammenian rocks (*1,* p. 103) and this report may be questionable.

Family DISPHYLLIDAE Hill

Disphyllidae *(partim)* HILL, 1939, p. 244;——SOSHKINA & DOBROLYUBOVA, 1962, p. 334.

Disphyllinae STUMM, 1949, p. 32;——WANG, 1950, p. 218; ——*(partim)* ROZKOWSKA, 1953, p. 9.

Peneckiellidae *(partim)* SOSHKINA, 1951, p. 101.

Phillipsastraeinae *(partim)* HILL, 1956, p. 279.

Phillipsastraeidae *(partim)* BULVANKER, 1958, p. 114;—— *(partim)* SOSHKINA & DOBROLYUBOVA, 1962, p. 336.
Hexagonariidae *(partim)* BULVANKER, 1958, p. 178.

Diagnosis.—Solitary, phacelloid, cerioid, and plocoid corals unified by trabecular fine structure of septa, undifferentiated dissepiments, and presence of epithecal wall in cerioid forms.

All genera placed in this family are characterized by the pattern of septal trabeculae labeled "convex upward" by KATO (1963, p. 592). Allied with this configuration are dissepimentaria formed of rows of relatively numerous, unspecialized, and small dissepiments which are more steeply inclined at the border of the tabularium than peripherally in the corallites.

In addition, all genera show differentiation of septa into first and second orders. Some genera show trends toward development of axial and periaxial series of tabulae. Some genera have species with carinate septa and some have species with septa dilated at the margin of the tabularium.

Remarks.—The massive members of this family are placed in the genera *Hexagonaria* and *Billingsastraea.*

Genus HEXAGONARIA Gürich

Hexagonaria GÜRICH, 1896, p. 171;——LANG & SMITH, 1935, p. 550;——LANG, SMITH, & THOMAS, 1940, p. 69;——STUMM, 1949, p. 33;——HILL, 1956, p. 280;——ROZKOWSKA, 1960, p. 14;——SOSHKINA & DOBROLYUBOVA, 1962, p. 334.
Prismatophyllum SIMPSON, 1900, p. 218.——WANG, 1950, p. 218.
Megaphyllum SOSHKINA, 1951, p. 108.
Tabellaephyllum (partim) SOSHKINA, 1951, p. 111.
Peneckiella (partim) SOSHKINA, 1951, p. 103.

Diagnosis.—Cerioid colonial corals having typically disphyllid septal fine structure with parallel trabeculae sloping upward and inward from their point of origin at epithecal wall separating corallites, which have peripheral calicinal platform and central pit on oral surface. Dissepiments numerous, globose, and generally tilted progressively inward as margin of tabularium is approached. Septa differentiated into first and second orders. In a primitive lineage *(Hexagonaria quadrigemina)* septa are attenuate, thickest at epithecal wall, and may be long, extending to center of tabularium, or shortened somewhat, leaving axial portion free. In a more advanced lineage *(H. hexagona)* septa are typically dilated at border of tabularium, and first-order septa generally extend to axis of corallite. In the earlier group, tabulae are frequently flat-topped and complete. In the advanced group, tabulae are commonly differentiated into axial and periaxial series. Budding generally nonparricidal, but commonly parricidal in *H. quadrigemina.*

Remarks.—I am placing in *Hexagonaria* all species which belong in the family Disphyllidae and which show a consistently cerioid colonial form. The genus thus encompasses many different species, united by configuration of their septal trabeculae and their lack of specialized dissepiments.

Species assignable to *Hexagonaria* have been placed in *Megaphyllum, Tabellaephyllum,* and *Peneckiella* by SOSHKINA, primarily on the basis of features of the tabularium. It is my opinion that length of septa is the factor most greatly influencing completeness of the tabulae and their division into axial and periaxial series. Since length of septa is generally variable within a species, I am unwilling to subdivide *Hexagonaria* on this basis.

Distribution.—*Hexagonaria* is found in Middle and Upper Devonian rocks of a number of continents.

The earliest reported occurrence of the genus is in France. In the lower Loire Valley it is found in the Erbray Limestone, of Emsian age (BARROIS, 1889), but in the Cotentin Peninsula of Normandy the genus is found in the Nehou Limestone, considered to be Siegenian in age by DANGEARD (1951, p. 61).

Hexagonaria occurs in Couvinian rocks of eastern North America and Australia *(12),* and is abundant in Givetian and Frasnian rocks of England, France, Belgium, Germany, Spain, Austria, Poland, Russia, China, and Australia. At this time the genus was truly cosmopolitan.

Genus BILLINGSASTRAEA Grabau

Phillipsastraea (partim) EDWARDS & HAIME, 1851, p. 447.
Phillipsastraea (Billingsastraea) GRABAU, 1917, p. 957.
Billingsastraea STUMM, 1949, p. 35;——HILL, 1956, p. 280;——SOSHKINA & DOBROLYUBOVA, 1962, p. 336;——OLIVER, 1964, p. 2;——*(partim)* STRUSZ, p. 547.
(non) Billingsastraea SCHOUPPÉ, 1958, p. 235.

Remarks.—No specimens ascribable to *Billingsastraea* have been found in Belgian Devonian faunas. The following discussion is included solely for the purpose of emphasizing this point.

Billingsastraea is regarded as a genus containing colonial corals with 1) plocoid colonial form, 2) universally attenuate septa with no tendency toward septal dilation, as pointed out by OLIVER (*24,* p. 3), 3) septal fine structure like that of *Hexagonaria,* with trabeculae near vertical in outer part of dissepimentarium, being progressively inclined axially and reaching maximum inclination at boundary of tabularium, and 4) gentle arching of each row of small, globose dissepiments *without* any differentiation into specialized dissepiments in inner dissepimentarium. Both the trabecular structure of the septa and arching of dissepiments are well shown in photographs figured by OLIVER (1964, pl. 1, fig. 4-5) and STUMM (1964, pl. 40, fig. 3).

The manner of naming by GRABAU of *Phillipsastraea (Billingsastraea) verneuili* (MILNE-EDWARDS & HAIME) has led to difficulties in defining the genus group. In discussing correlation of the *Hypothyridina* fauna of the Tully Limestone in New York, he listed species occurring with the Frasnian *Hypothyridina cuboides* fauna of Europe, and included *P. (B.) verneuili.* He thus defined *Billingsastraea* as a subgenus of *Phillipsastraea,* by monotypy fixing *P. verneuili* as the type species. GRABAU wrongly intimated that this species is found in Upper Devonian rocks of Europe (*10,* p. 957).

The type specimen of *Billingsastraea verneuili* was labeled by MILNE-EDWARDS & HAIME (*22,* p. 447) as Devonian, Wisconsin, U.S.A. STUMM (*40,* p. 35) stated that the specimen was probably collected from glacial drift, and originated in strata equivalent to the Onondaga Formation in Ontario or northern Michigan. The type specimen of the species supposedly rests in the de Verneuil collection at the École Supérieur des Mines in Paris, where to date the specimen has not been located.

SCHOUPPÉ regarded *Billingsastraea* as a *"Phillipsastraea* without horseshoe dissepiments" (1958, p. 160), stating that in doing so he was following the diagnosis of STUMM. However, STUMM stated that "septa are not dilated at the border of the tabularium as they are in *Phillipsastraea,*" (1949. p. 35). On the other hand, HILL (1958, p. 280) asserted that *Billingsastraea* is "like *Phillipsastraea* but septa carinate and attenuate; tabulae flat-topped domes." These descriptions fail to take account of basic differences in septal fine structure and architecture of the dissepiments.

There should be no confusion in distinguishing between individuals assignable to *Billingsastraea* and those without horseshoe dissepiments placed in *Phillipsastraea.* The latter are still characterized by dilated septa displaying fan-shaped trabecular configurations, with the area of divergence in the inner dissepimentarium. Other less easily defined criteria, such as generally smaller size and smaller number of septa, also serve to distinguish *Phillipsastraea.* No members of the *Billingsastraea* genus group are known from the Middle and Upper Devonian rocks of Belgium, and possibly of Europe as a whole.

BIOMETRY

The genera and species reported in this article have been studied primarily from a qualitative morphologic point of view. However, it is of considerable value to have a numerical expression of the range of intraspecific variation deemed acceptable by a given author.

For all species considered here, data regarding number of septa and diameter of tabularium are presented. For those in which only a small sample was available, data have been summarized in the description of the species. The number of colonies, number of corallites, colony mean values for number of septa (n), and diameter of tabularium (Dt), and the total observed range of variation of these last two features are all given.

For species in which a moderately large number of specimens was available, scatter diagrams have been constructed. In each the mean value of every available colony is presented with respect to its diameter of tabularium (Dt) and number of septa (n). In addition, the total number of corallites (N) and the grand mean values of diameter ($\overline{Dt}$) and number of septa ($\bar{n}$) are recorded. The desired goal in the collection of these data was to examine at least 20 corallites in 20 colonies, but this was possible in only one species. Thus, the other diagrams represent something of a compromise demanded by the limiting factor of available sample size.

The diagrams depart somewhat from those presented by various other authors, primarily owing to specialized problems of interpreting the massive colonial forms. The septal number *(n)* represents all septa, rather than major septa only. In several species, some individuals were encountered in which major and minor septa could not be differentiated. For uniformity of treatment, all septa were counted in all species.

In massive Rugosa, total diameter of the individual corallite is much less meaningful than for other colonial or solitary forms. It is difficult to determine accurately the diameter of a corallite in a cerioid or pseudocerioid colony, and still more difficult to make this measurement in plocoid colonies. In addition, in massive colonies total diameter is greatly dependent on relative rates of reproduction and growth. Corallites in a central position are constricted in their growth expansion by those disposed laterally. As a result, I have based my considerations of size in all massive corals exclusively on diameter of the tabularium.

SYSTEMATIC PALEONTOLOGY

Genus PHILLIPSASTRAEA d'Orbigny

PHILLIPSASTRAEA HENNAHI (Lonsdale)

Figures 5, *1a,b*; 8, *1a-d*

Astraea hennahi LONSDALE, 1840, p. 697, pl. 58, fig. 3, 3a, 3b.

Phillipsastraea hennahi D'ORBIGNY, 1849, p. 12;——MILNE-EDWARDS & HAIME, 1850, p. lxvi;——SMITH, 1917, p. 288, pl. 22;——SMITH, 1945, p. 36, pl. 19;——SCHOUPPÉ, 1958, p. 235, figs. 20, 21.

Smithia hennahi MILNE-EDWARDS & HAIME, 1851, p. 171;——MILNE-EDWARDS & HAIME, 1853, p. 240, pl. 54, fig. 4.

Diagnosis.—Type species of *Phillipsastraea* by subsequent designation (MILNE-EDWARDS & HAIME, 1850, p. lxvi). Variable, with long first-order septa characterized by spindle-shaped dilation. Colonial form varying from pseudocerioid to plocoid, specialization of innermost dissepiments from weakly arched to near horseshoe form; tabulae differentiated into axial flat-topped series and sagging periaxial series.

Type specimen.—*Astraea hennahi* LONSDALE, 1840, p. 697, Geological Society Coll. no. 6185 in Museum of Practical Geology, Geological Survey of Great Britain, London. This specimen was identified by SMITH (1917, p. 284) with certainty as that forming the basis of figure 3 of LONSDALE (1840).

In the type corallum of *Phillipsastraea hennahi*, 14 corallites yield a mean number for septa of 26.2 and a mean diameter of tabularium of 2.56 mm. The total observed ranges are 24-28 septa and 2.3-3.0 mm. The lectotype was described in detail by SMITH *(32, 33)* but it can be added that wall remnants present between some portions of the corallites are septal in construction (trabecular), and specialized dissepiments are present at the innermost portion of the dissepimentarium, accompanied by a strong upbowing of the rows of dissepiments. I was not able to discern a typical row of uniform upbowed dissepiments such as those usually referred to as horseshoe dissepiments.

Description.—In 17 colonies of *Phillipsastraea hennahi* from Belgium, the grand means are 25.0 for number of septa and 2.5 mm. *(Dt)* for the total number of corallites (239) examined (Fig. 9). The total observed range in number of septa is 20-32, and in diameter *(Dt)* is 1.9-3.2 mm. The coralla means range from 22.9 to 30.5 *(n)* and from 2.0 to 2.8 mm. *(Dt)*.

The colonial form of the species is variable, pseudocerioid, plocoid, and intermediate forms between the two have been noted in the fauna.

The external form of septa is highly characteristic of the species. First-order septa extend almost to the axis, where they may join, whereas second-order septa never extend into the tabularium. All septa are dilated, the amount of dilation being variable; in some specimens dilation is marked enough to form a wall around the tabularium (Fig. 8, *1a,b*), but in other colonies dilation is much less marked. In some individuals the second-order septa are essentially undilated. Weak septal carinae are developed in some colonies (Fig. 8,*1c*); however, forms showing strong septal dilation are invariably noncarinate.

Development of specialized dissepiments is also variable in this species. Dissepiments similar in appearance, although not in uniformity, to horseshoe dissepiments can be noted in some individuals (Fig. 8, *1a*), whereas others show less arching and more regularity of form. At the extreme limit of variability, no arched or specialized dissepiments are to be seen (Fig. 5,*1b*; 8,*1d*). Variability in size and number of dissepiments is also marked, as demonstrated by the just-cited figures. The tabularia however are rather uniform in aspect, with development of flat-topped axial series and sagging peripheral series. (Fig. 5,*1b*; 8,*1a,d*).

Septal fine structure is typical for the genus, with vertical fans of divergent septal trabeculae in

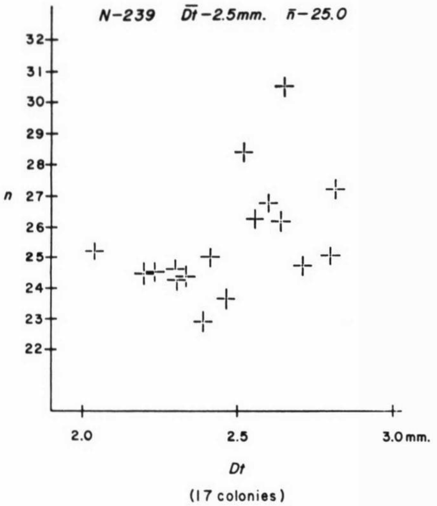


FIG. 9. *Phillipsastraea hennahi.* Scatter diagram of mean number *(n)* of septa × mean diameter *(Dt)* of tabularium for each of 17 colonies. $\overline{Dt}$ and $\overline{n}$ are grand mean values for total number *(N)* of corallites examined.

the area of dilation of the septa. However, the tightness of such fans and bundles of trabeculae varies, generally forming tight fans where the degree of specialization of dissepiments is marked and forming looser fans where there are fewer, larger dissepiments or less specialization of dissepiments, or both (Fig. 8,*1d*).

Remarks.—A group as variable as the one here regarded as species *Phillipsastraea hennahi* presents taxonomic difficulties simply because of the variation. Most probably this group would be regarded by some paleontologists as containing more than a single species, but no boundaries were discernible by me.

It also seems that all interrelated are 1) nature of trabecular fans in the septa, 2) degree of specialization of innermost dissepiments, and 3) number and relative size of the dissepiments, as suggested above. If assumption is made that number and relative size of dissepiments (within limits of variation of a species) is a function of the rate of growth (i.e., rapid growth producing fewer and larger dissepiments), then it follows that trabecular fans become tighter, and a marked calicinal ridge and horseshoe dissepiments are developed where growth is slower. Data are insufficient at present to support or deny this hypothesis.

Phillipsastraea hennahi is widespread throughout Europe and is an excellent indicator of late Frasnian age.

Distribuution.—Observed occurrences of *Phillipsastraea hennahi* in Belgium are limited to the F_{2i} level of the Dinant Basin. This species should also be present in the upper Frasnian of the Namur Basin.

PHILLIPSASTRAEA GOLDFUSSI (de Verneuil & Haime)

Figures 10,*1a-d*; 11,*1a,b*

Cyathophyllum ananas GOLDFUSS, 1826, p. 60, pl. 19, fig. 4a.

Acervularia goldfussi DE VERNEUIL & HAIME, p. 161;—— MILNE-EDWARDS & HAIME, 1851, p. 417;——MILNE-EDWARDS & HAIME, 1853, p. 236, pl. 53, fig. 3, 3a.

Phillipsastraea ananas FRECH, 1885, p. 49, pl. 2, fig. 4, 4a, 4b.

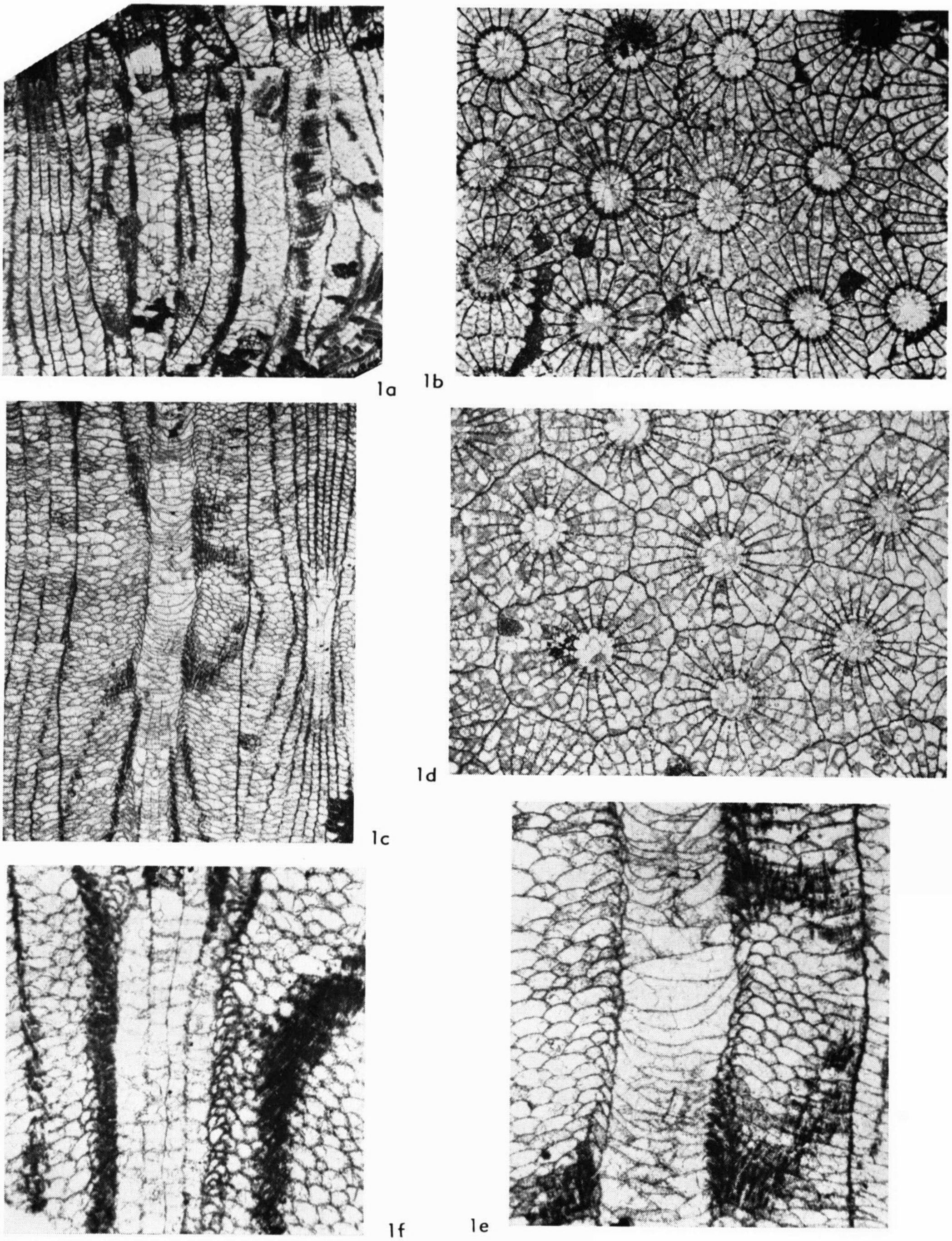
Phillipsastraea goldfussi ROZKOWSKA, 1953, p. 62, pl. 8, fig. 5-6;——SCHOUPPÉ, fig. 25-26.

Diagnosis.—Variable species occurring most commonly in pseudocerioid colonies with small tabularia and few septa. Tabulae generally complete and widely spaced. Numerous small globose dissepiments present.

Description.—In 14 coralla belonging to the species (Fig. 12), 275 corallites produce grand mean values of 23.8 *(n)* and 1.8 mm. *(Dt)*. The range in coralla mean values is 22-28.5 septa and 1.6-2.2 mm. *(Dt)*. The total observed range for all corallites is 22-32 septa and 1.4-2.5 mm. *(Dt)*. The species occurs most typically in pseudocerioid colonial form marked by a regularity of polygonal corallite sides, but some individuals show a partial loss of pseudocerioid form.

First-order septa most commonly extend from one-half to three-fourths through the tabularium, but may extend to the axis and join (Fig. 10,*1b,d*). Second-order septa invariably fail to extend beyond the border of the tabularium. In almost all colonies, septa show some weak dilation in the innermost part of the dissepimentarium. Weak septal carinae are commonly developed as a result of inflation or lateral growth of septal trabeculae. Walls present in complete or incomplete form are always septal in construction and may also bear weak carinae where such carinae are present in the septa. Walls show a weakly zigzag path, and septa are normally in an offset position (Fig. 10,*1b,d*; 11,*1a*).

The dissepimentarium is filled with rows of approximately 4-7 dissepiments of small size and globular nature. The innermost one to three rows are composed of dissepiments which are smaller and more highly inflated than other, unspecialized



Phillipsastraea goldfussi

FIG. 10. *Phillipsastraea goldfussi* (DE VERNEUIL & HAIME) from Upper Devonian (Frasnian unit F_{2i}) of **Belgium.**

1a,b. Longitudinal and transverse sections of specimen from Beauchateaux Quarry, Senzeille (Sorauf col., USNM), showing development of septal dilation at outer edge of tabularium with resultant formation of inner wall, both ×4.

dissepiments. The tabularium is characteristically filled with widely spaced, generally complete tabulae, sagging aborally (Fig. 10,*1c*). Tabellae may be developed as lateral plates leaning against walls of the tabularium.

The septal fine structures are consistent with those found throughout the genus and family. However, fans of septal trabeculae noted in this species are commonly somewhat asymmetrical, displaying greater inclination of trabeculae on the axial side.

Remarks.—This species is closely related to, and greatly resembles *Phillipsastraea pentagona*, from which it can be differentiated by its slightly larger size and more numerous septa. The two species together are somewhat dissimilar from most other species of the genus, differing in smaller size and smaller number of septa, as well as a lesser tendency toward development of spindle-shaped septal dilation and development of plocoid colonial form. In most other characteristics, however, this group resembles other species of *Phillipsastraea*, and thus I have not separated it.

This species was first named *Cyathophyllum ananas* by GOLDFUSS in 1826. In 1851, MILNE-EDWARDS & HAIME, apparently (although not so stating) influenced by the generic classification (*Acervularia*) current at that date, suppressed the species name *ananas* for *goldfussi*. It must be assumed that this step was taken owing to the presence of the Linnean species *A. ananas* from the Silurian of Gotland. In 1851, MILNE-EDWARDS & HAIME also fixed the type for their species as the specimen illustrated by figure 4a on plate 19 published by GOLDFUSS (1826, p. 60). Prior to this, DE VERNEUIL & HAIME (1850, p. 161) had employed the name *A. goldfussi* in a faunal list of Devonian species from Spain.

Recent workers (ROZKOWSKA, 1953, p. 62; SCHOUPPÉ, 1958, p. 236) have employed the nomenclature of MILNE-EDWARDS & HAIME (1851) although FRECH (1885, p. 49) employed the name *ananas* for this species.

Distribution.—Observed occurrences of the species were from the F_{2i} and F_{2j} levels of the Dinant Basin and from the F_{2II} and questionably from the F_{2II} horizon in the Namur Basin.

PHILLIPSASTRAEA PENTAGONA (Goldfuss)

Figures 13,*1a-f*; 14,*1a-c*

Cyathophyllum pentagonum GOLDFUSS, 1826, p. 60, pl. 19, fig. 3.

Acervularia pentagona MILNE-EDWARDS & HAIME, p. 238, pl. 53, fig. 5, 5a, 5b.

Phillipsastraea pentagona FRECH, 1885, p. 54, pl. 3, fig. 6-10, pl. 8, fig. 3;——ROZKOWSKA, 1953, p. 64, pl. 8, fig. 7.

Diagnosis.—*Phillipsastraea* characterized by a consistently very small diameter of tabularium and the smallest number of septa known for the genus. Species shows little or no tendency toward development of plocoid colonial form, but compact inner wall is commonly formed at border of tabularium. Tabulae generally complete and widely spaced, and only moderate specialization of dissepiments is known within the Belgian fauna.

Description.—*Phillipsastraea pentagona* is marked by small size of corallites and a small number of septa. In 30 colonies (Fig. 15) 614 corallites yield a grand mean value of 19.9 septa and 1.1 mm. for diameter of the tabularium. The range of means for coralla is 16.6 to 21.4 *(n)* and 0.58 to 1.6 mm. *(Dt)*. The total observed range for all corallites is 16 to 24 septa and 0.55 to 1.8 mm. *(Dt)*.

More meaningful observations can be made if the data for *Phillipsastraea pentagona minima* (see below) are removed. In the 21 colonies remaining, 420 corallites provide grand mean values of 20.3 septa and 1.3 mm. *(Dt)*. The mean values of the 21 coralla range from 19 to 21.5 septa and 1.0 to 1.6 mm. *(Dt)*. The total observed range is 16 to 24 septa and 0.9 to 1.8 mm. *(Dt)*.

The species occurs in the pseudocerioid colonial form, with corallites of small diameter retaining a more regular polygonal shape, whereas colonies with larger corallites have a less regular shape (Fig. 13,*1a,c,e*). Walls are septal in construction, and tend to a more or less well-developed zigzag path.

FIG. 10. *(Explanation continued from facing page.)*

1c-e. Longitudinal and transverse sections of very typical corallum from Neuville Quarry, Neuville (Sorauf coll., USNM), *1c,d*, ×4, *1e* (part of *1c*), ×9.

1f. Longitudinal section of specimen also from Neuville Quarry (Sorauf coll., USNM) showing open fans of septal trabeculae and no specialization of dissepiments, ×9.

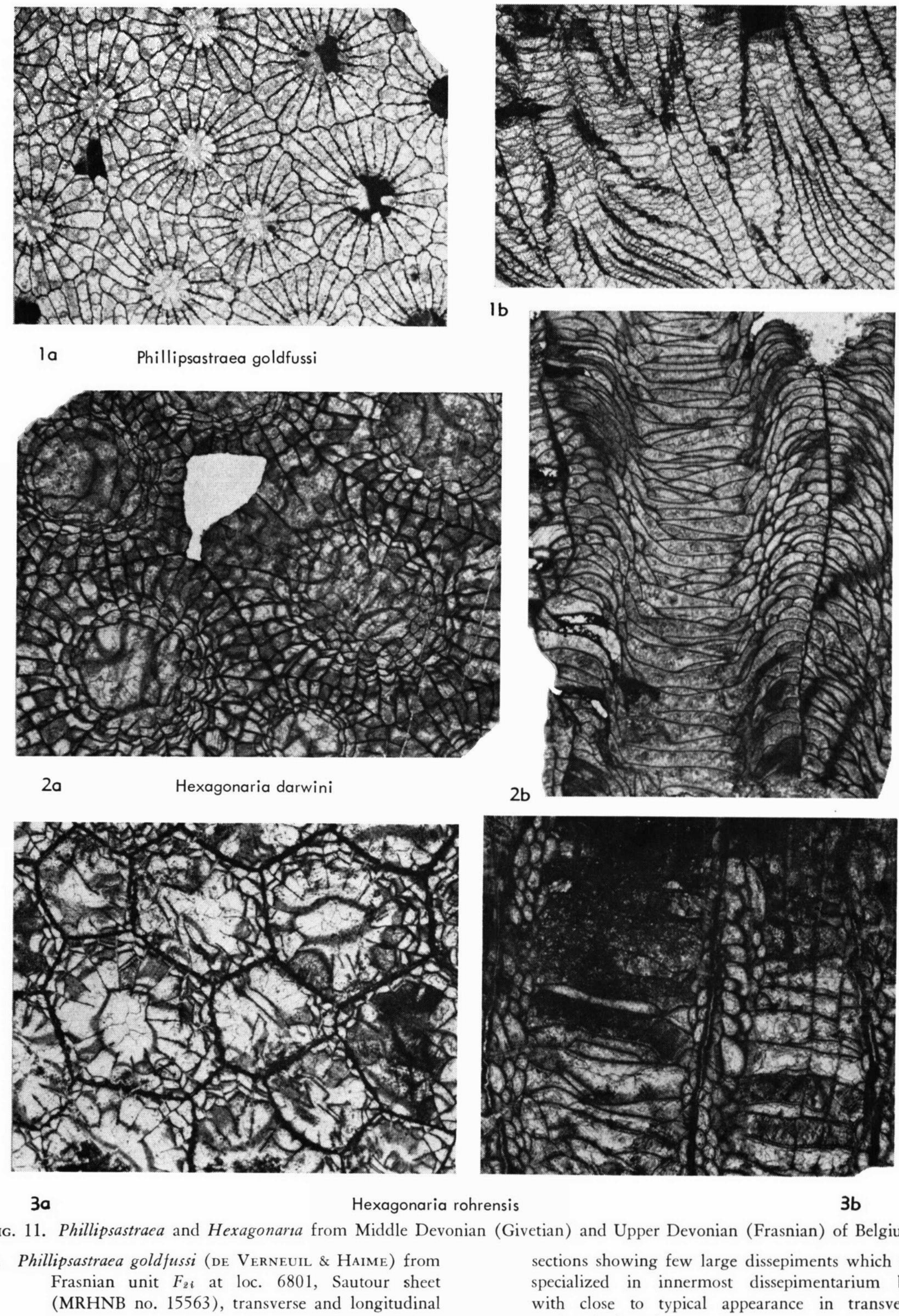


FIG. 11. *Phillipsastraea* and *Hexagonaria* from Middle Devonian (Givetian) and Upper Devonian (Frasnian) of Belgium.

1. *Phillipsastraea goldfussi* (DE VERNEUIL & HAIME) from Frasnian unit F_{2i} at loc. 6801, Sautour sheet (MRHNB no. 15563), transverse and longitudinal sections showing few large dissepiments which are specialized in innermost dissepimentarium but with close to typical appearance in transverse section, both ×4.

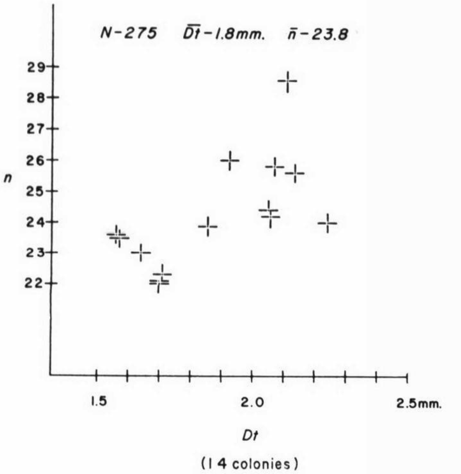


FIG. 12. *Phillipsastraea goldfussi.* Scatter diagram of mean number *(n)* of septa × mean diameter *(Dt)* of tabularium for each of 14 colonies. $\overline{Dt}$ and $\bar{n}$ are grand mean values for total number *(N)* of corallites examined.

First-order septa usually extend to the axial area of the corallites and join there, but numerous examples were noted in which both first- and second-order septa fail to extend past the border of the tabularium. Septal dilation is common in the species and in its most extreme development forms a thin, compact inner wall (Pl. 7, fig. 5 around the tabularium. Forms with such a wall may have first-order septa that do not extend into the tabularium.

The dissepimentarium contains numerous small, globose dissepiments, 7 to 9 per row, with innermost rows commonly smaller and more globose, forming a slightly arched surface. Tabulae are most commonly widely spaced, complete, and either slightly arched adorally or slightly sagging aborally. Accessory plates are present at numerous levels (Fig. 13,*1b,d*).

The septal fine structure varies. Forms without an inner wall have septal trabeculae arranged in symmetrical fans in the innermost portion of the dissepimentarium. Coralla with the inner wall formed by dilation of a single row of vertical trabeculae have neither trabecular fans nor accompanying specialization of dissepiments (Fig. 13,*1f*).

Remarks.—This species most closely resembles *Phillipsastraea goldfussi* in its larger size and more numerous septa. Formation of the inner wall has previously been discussed in the section on morphology.

The species is widespread in Europe, reported from Poland in the east to Devonshire in the west, and is an excellent guide to upper Frasnian rocks.

Distribution.—Observed occurrences of this species are in F_{2i} and F_{2j} levels of the Dinant Basin and the F_{2II} and F_{2III} beds of the Namur Basin.

PHILLIPSASTRAEA PENTAGONA MINIMA Rozkowska

Figure 14,*1a-c*

Phillipsastraea pentagona minima ROZKOWSKA, 1953, p. 66, fig. 38, pl. 8, fig. 9.

Diagnosis.—Subspecies of *Phillipsastraea pentagona* marked by smaller size and uniform 20 septa. Compact inner wall developed in almost all Belgian forms placed in this subspecies.

Description.—Grand mean values for 194 corallites in 10 colonies (Fig. 16) are 18.9 for number of septa and 0.73 mm. for diameter *(Dt)*. The means of the 10 colonies vary from 16.6 to 19.8 septa and 0.58 to 0.8 mm. for *Dt*. The total observed range in all corallites was 16 to 22 septa and 0.5 5to 0.85 mm. *(Dt)*.

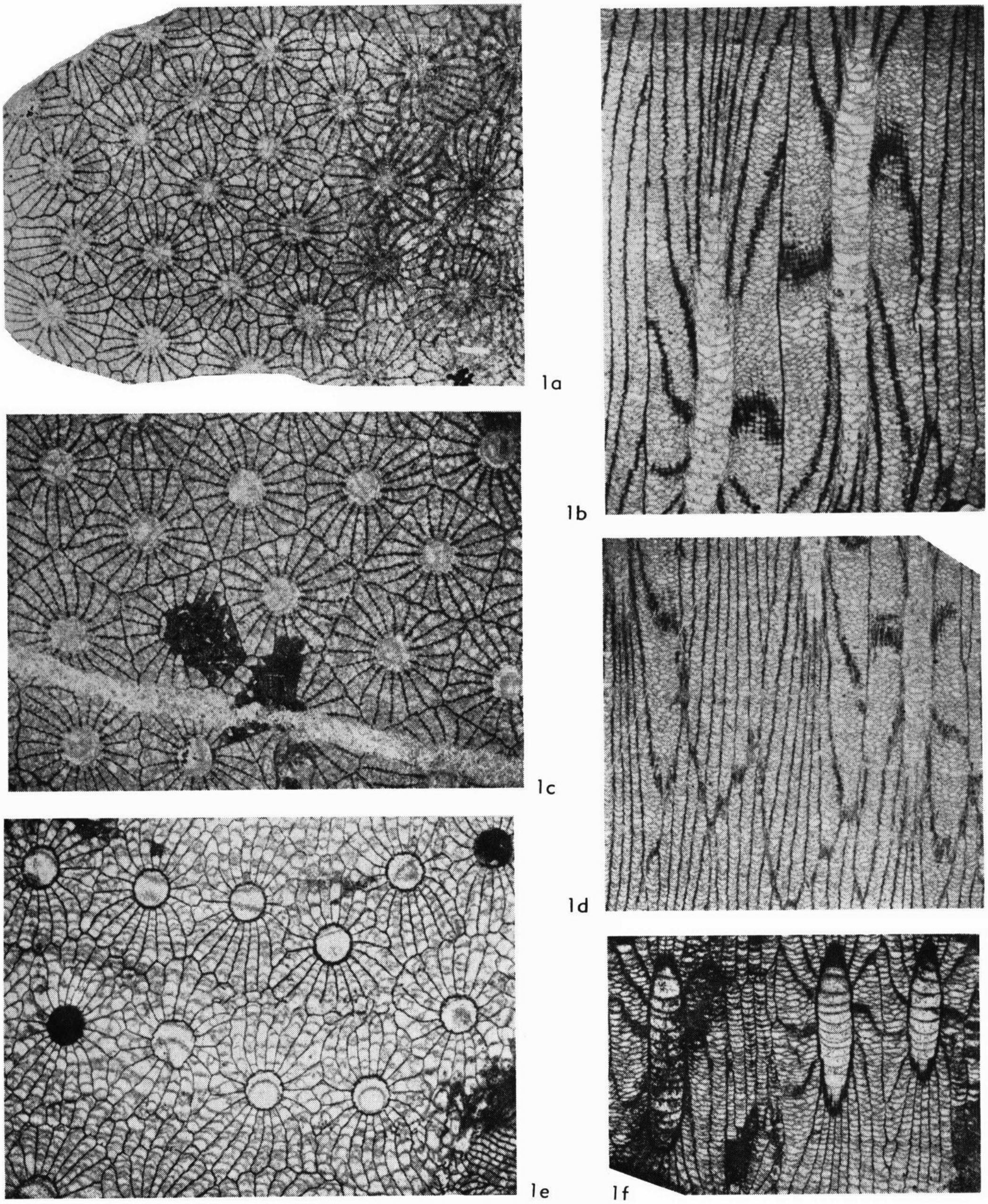
It is this small size, coupled with the presence of a compact inner wall surrounding the tabularium that makes the subspecies distinctive. First-order septa uniformly extend through the inner wall to join in the axial region of the corallites (Fig. 14,*1a,b*). Little or no specialization of dissepiments is present in this group (Fig. 14,*1c*).

Remarks.—This group of very small corals is remarkable for uniform development of an inner wall and makes an excellent index fossil when

FIG. 11. *(Explanation continued from facing page.)*

2. *Hexagonaria darwini* (FRECH) from Frasnian unit F_{2IIIb} at loc. 1, Champion sheet (MRHNB no. 16713) characterized in transverse section *(2a)* by wide spacing of its attenuate septa which leave a wide open space in the tabularium and in longitudinal section *(2b)* by very uniform flat-bottomed septa and elongate flattened dissepiments, both ×4.

3. *Hexagonaria rohrensis* GLINSKI, Old Collard Quarry, Couvin (Sorauf coll., USNM), basal Gi_b; in transverse section *(3a)* showing few short attenuate septa, ×4, whereas in longitudinal section *(3b)* are noted paucity of dissepiments and flat complete tabulae, ×6.



Phillipsastraea pentagona

FIG. 13. *Phillipsastraea pentagona* (GOLDFUSS) from Upper Devonian (Frasnian unit F_{2i}) of Belgium.

1a,b. Transverse and longitudinal sections of typical specimen from Neuville Quarry, Neuville (Sorauf coll., USNM), with undulating intercorallite wall, irregular sagging tabulae, and septal trabeculae in open fans, ×4.

1c,d. Transverse and longitudinal sections of specimen from Neuville railroad trench (Sorauf coll., USNM), with relatively uniform pentagonal corallite outline, weakly developed trabecular fans, and irregular uparched tabulae, ×4.

1e,f. Transverse and longitudinal sections of colony from loc. 6839, Senzeille sheet (MRHNB no. 15760), with well-developed inner wall surrounding tabularium and complete, evenly spaced tabulae with aboral sag, ×4.

found. Rozkowska *(26)* reported it from an upper level of the upper Frasnian of Poland.

Distribution.—The observed occurrences of this subspecies were limited to the F_{2i} of the Dinant Basin, and the F_{2IIIc} beds of the Namur Basin.

PHILLIPSASTRAEA MACROMMATA (F. A. Roemer)

Figure 14,*2a-c*

Acervularia macrommata F. A. Roemer, 1855, p. 33, pl. 6, fig. 22.

Pseudoacervularia macrommata Rozkowska, 1953, p. 49, pl. 7, fig. 5-7.

Diagnosis.—*Phillipsastraea* with mean 29 septa and tabularia with diameter in the 3-mm. size range. The species is marked by heavy dilation of all septa near the outer border of the tabularium, and the development in some of uniform specialized dissepiments.

Description.—*Phillipsastraea macrommata* is of medial to large size for the genus. A total of 243 corallites in 15 colonies yield grand mean values of 28.7 *(n)* for septa and 3.1 mm. for *Dt.* The coralla means range from 24.5 to 31.7 septa and 2.2 to 3.7 mm. for *Dt.* (Fig. 17). The total observed range for all corallites is 22 to 34 *(n)* and 2.0 to 4.1 mm. *(Dt).* The species occurs in the pseudocerioid colonial form exclusively, and is characterized by marked dilation of both major and minor septa near the border of the tabularium (Fig. 14,*2a*). The septa are thin in the outer part of the corallite, swell to 4 or 5 times the normal width, and major septa then continue into the tabularium as thin blades which are commonly joined at the axis of the corallite. The intercorallite walls are septal in construction and have zigzag path similar to that of other species of the genus.

In longitudinal section are seen dissepimentaria (each approximately one-fourth of total diameter) filled with numerous dissepiments that are irregular in size. Specialization of dissepiments beneath septal trabecular fans is somewhat variable. In several coralla, uniformity of size and degree of inflation of the row of dissepiments directly under the tight fans of divergent septal trabeculae is such that they truly approach the shape of horseshoe dissepiments, whereas others show little differentiation (Fig. 14,*2c*). In addition, there are generally two or three rows of dissepiments between the most-arched row and the border of the tabularium.

The tabularia are typical for the long-septate species of the genus, with an axial series of flat-topped tabulae and numerous lateral plates leaning on the axial series and the edge of the tabularium.

The septal fine structure, as noted above, contains symmetrical, tight fans of divergent trabeculae with the axis of divergence at a distance from the border of the tabularium.

Remarks.—*Phillipsastraea macrommata* does not appear to be closely related to other species of the genus in the Belgian fauna. In addition, it is quite variable in the amount of septal dilation and in specialization of dissepiments. This species was found at one locality only, where it is abundant (Carriére des Beauchateaux, near Senzeilles).

Distribution.—*Phillipsastraea macrommata* was noted only in the F_{2i} and F_{2j} beds of the central part of the central part of the Dinant Basin.

Genus HEXAGONARIA Gürich

HEXAGONARIA HEXAGONA (Goldfuss)

Figure 4,*1a-d,2a-c*

Cyathophyllum hexagonum Goldfuss, 1826, p. 61, pl. 20, fig. 1a,b.

Hexagonaria hexagona Gürich, 1896, p. 171;——Lang, Smith, & Thomas, 1940, p. 69.

Diagnosis.—*Hexagonaria* with median 36 to 38 septa, well-developed polygonal outline of corallites, marked septal dilation in inner dissepimentarium, and axial and periaxial tabulae.

Description.—*Type specimen* (type of genus and species) Paleontological Museum, University of Bonn, Germany. Lectotype is one of two specimens thought to be originals of pl. 20, fig. 1a?,b, of "Petrifactae Germaniae," A. Goldfuss, 1826. In transverse section corallites in corallum yield mean values of 39.1 septa and 6 mm. for *Dt.* Observed range in these individuals is 5 to 8 mm. for *Dt* and 36 to 44 for *n.* First-order septa reach to the axis, are deflected laterally, and are in lateral contact with neighboring septa. Second-order septa reach only to the border of the tabularium. All septa are rather strongly dilated in the area of the border of the tabularium, forming a buttressed margin to the tabularium in some individuals. Septa show inflated trabeculae; thus in cross section weak carinae are present in some corallites, although absent in others. The intercorallite walls are quite straight, show good development of epitheca, and generally show septa

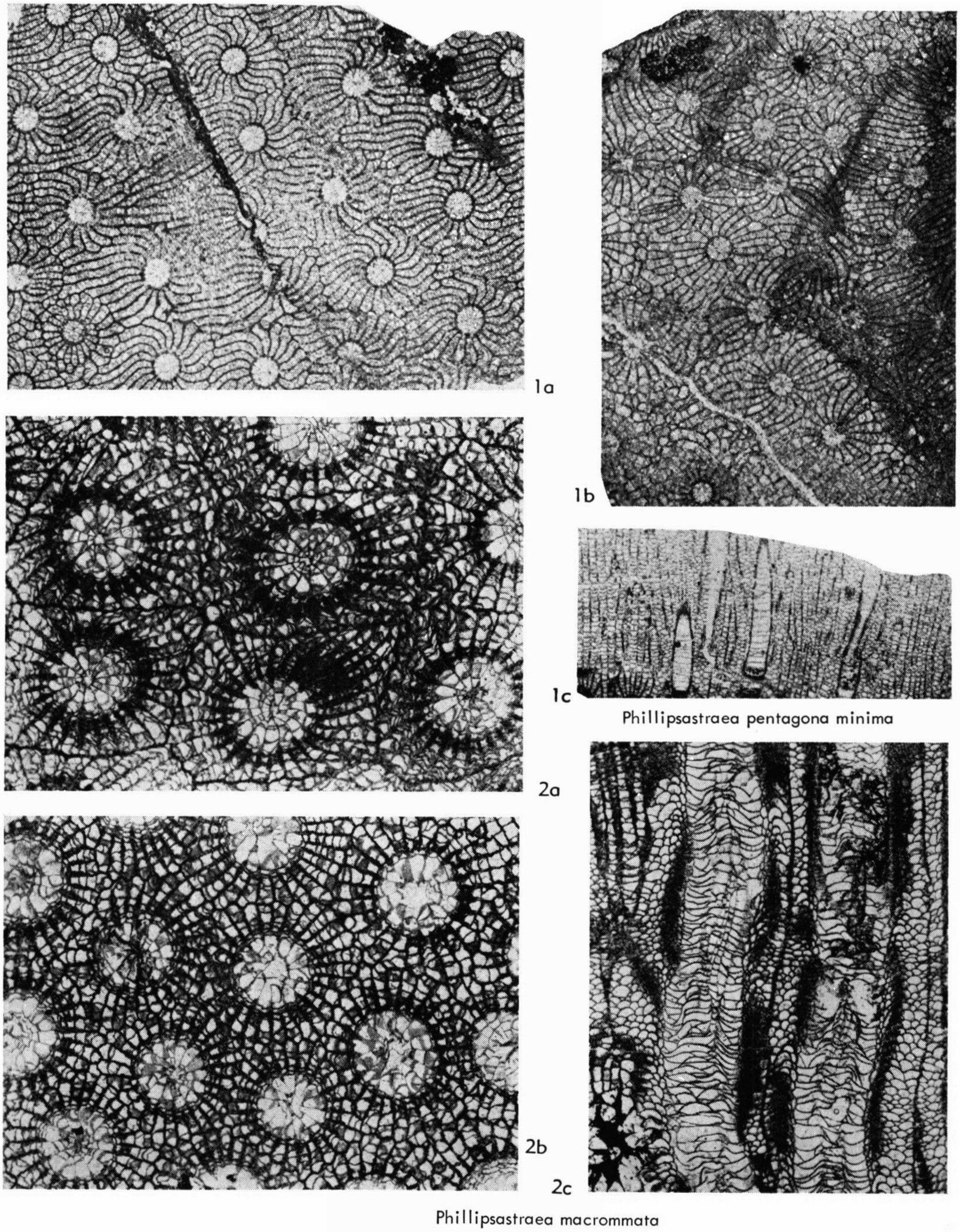


FIG. 14. *Phillipsastraea* from Upper Devonian (Frasnian uunit F_{2i}) at Senzeille, Belgium.

1. *Phillipsastraea pentagona minima* ROZKOWSKA.——*1a.* Transverse section of specimen from loc. 6816a,b, Senzeille sheet (MRHNB no. 15686) showing clearly presence of inner wall and ?rejuvenation of corallite at upper left, ×4.——*1b,c.* Transverse and longitudinal sections of specimens from loc. 6854, Senzeille sheet (MRHNB no. 15817), *1b,* showing presence of inner wall and apparent doubling of intercorallite walls at numerous places; *1c* showing complete straight tabulae, both ×4.

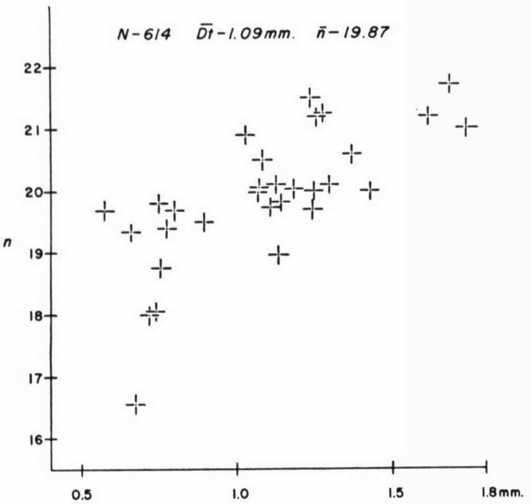


FIG. 15. *Phillipsastraea pentagona.* Scatter diagram of mean number *(n)* of septa × diameter *(Dt)* of tabularium for each of 30 colonies. $\overline{Dt}$ and $\overline{n}$ are grand mean values for total number *(N)* of corallites examined.

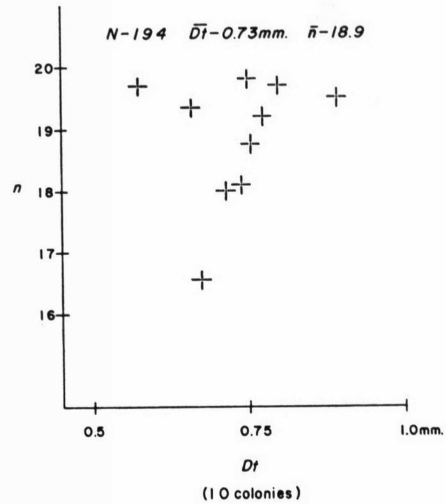


FIG. 16. *Phillipsastraea pentagona minima.* Scatter diagram of mean number *(n)* of septa × diameter of tabularium *(Dt)* for each of 10 colonies. $\overline{Dt}$ and $\overline{n}$ are grand mean values for total number *(N)* of corallites examined. Note also that the colonies diagrammed here are included at the left side of Fig. 15.

inserted in opposition in neighboring corallites. In transverse section, dissepiments appear numerous and irregular in size, on the average forming 6 or 7 rows from epitheca to tabularium.

In a slightly oblique longitudinal section, septal fine structure is well shown. Septal trabeculae are nearly parallel to epitheca in the outer part of the dissepimentarium and slope gradually inward to 60°-70° axial inclination at the border of the tabularium. The dissepiments are numerous, globose, and decrease in size adaxially. Their orientation is perpendicular to the septal trabeculae, and thus they are horizontal near the epitheca and tilted progressively inward as the tabularium is approached. The section is not truly suitable for examination of tabulae, but a suggestion of differentiation into axial and periaxial series is present.

Remarks.—LANG & SMITH (1935, p. 550) chose as lectotype the specimen figured by GOLDFUSS on pl. 20, fig. 1a,b, in "Petrifactae Germaniae" in 1826. The museum label on the specimen sectioned reads "Orig. Goldfuss, taf. XX, fig. 1a (?), b." In my opinion, of the two specimens in the box, neither one corresponds exactly to the figures in "Petrifactae Germaniae." However, one colony has marginal corallites in a recumbent or recurved condition, as shown in Fig. 1b, suggesting that the artist used the uncut specimen as a model for Fig. 1b. Thus, the specimen which has been thin-sectioned would have been the model for Fig. 1a. The locality and horizon on the specimen identity card is listed as "M. Dev.-Bensberg." As a result of experience with the Belgian forms of the genus, I question the Middle Devonian age of the specimen. In Belgium, no *Hexagonaria* with septal dilation appears lower than the middle Frasnian F_{2g} horizon, where *H. hexagona* is first found.

FIG. 14. *(Explanation continued from facing page.)*

2. *Phillipsastraea macrommata* (F. A. ROEMER) from from Beauchateaux Quarry (Sorauf coll., USNM). ——*2a.* Transverse section of very typical corallum showing marked septal dilation at outer edge of tabularium, ×4.——*2b,c.* Transverse and longitudinal sections showing uneven development of septal dilation *(2b)* and axial and periaxial series of tabulae *(2c)* with tight fans of septal trabeculae (top of photo) and weak development of specialized dissepiments near inner margin of dissepimentarium, both ×4.

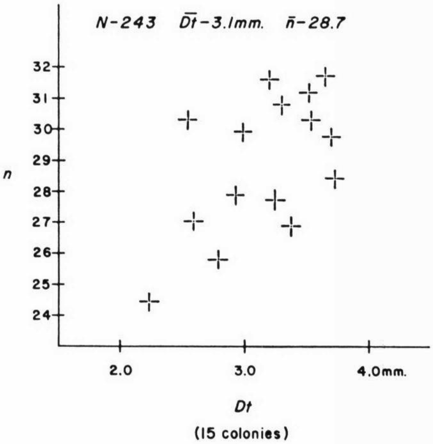


FIG. 17. *Phillipsastraea macrommata.* Scatter diagram of mean number *(n)* of septa × diameter *(Dt)* of tabularium for each of 15 colonies. $\overline{Dt}$ and $\bar{n}$ are grand mean values for the total number *(N)* of corallites involved.

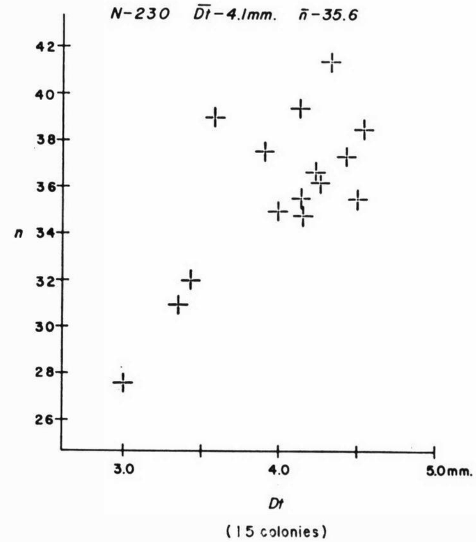


FIG. 18. *Hexagonaria hexagona.* Scatter diagram of mean number *(n)* of septa × diameter of tabularium *(Dt)* for each of 15 colonies. $\overline{Dt}$ and $\bar{n}$ are grand mean values for the total number of corallites *(N)*.

Description.—Belgian Fauna. The Belgian specimens of *Hexagonaria hexagona* have a grand mean value of 35.6 septa *(n)* and 4.0 mm. for diameter *(Dt)* in 230 corallites of 15 colonies. The coralla means range from 27.6 to 41.4 septa and 3.0 to 4.6 mm. for *Dt.* The total observed range for all corallites is 24 to 48 septa and 2.3-6.0 mm. for the diameter *(Dt)* (Fig. 18).

First-order septa are uniformly long, reaching to or almost to the axis of the corallite, where the ends of septa are deflected. Dilation of septa is variable, but a majority of colonies show some septal dilation at the inner margin of the dissepimentarium, reaching approximately 2 times normal width. Walls in this species are commonly rather straight, especially when septa in neighboring corallites are in the opposition position (Fig. 4,*1b,d,2b*).

The tabularium is characterized by axial and periaxial series of tabulae. Axial tabulae are most commonly somewhat arched and flat-topped (Fig. 4,*1c*), while periaxial plates sag aborally with globose, arcuate tabellae resting upon them. This differentiation is typical of species in which the major septa reach all the way to the axis of the corallite.

Septal fine structure is typically disphyllid, with trabeculae either paralleling or making a small angle with the epitheca and bending progressively inward as the dissepimentarium is traversed, with a maximum angle of inclination of 70° to 88° present at the outermost portion of the tabularium (Fig. 4,*2c*).

Remarks.—*Hexagonaria hexagona* is the most common species of colonial coral in the medial Middle Frasnian (F_{2h-i}), and indeed is commonly the only colonial species encountered in and above the F_{2h} bioherms and basal F_{2i} shales of the southern margin of the Dinant Basin. It is a species without much variability in morphologic characteristics. The notable variation is found in the number and amount of dilation of septa. Thus it bears a striking resemblance to the type specimen described by GOLDFUSS. This species is restricted to the Middle Frasnian in Belgium, leading to the conclusion that the form described by GOLDFUSS as Middle Devonian may be mislabeled as to horizon.

Distribution.—*Hexagonaria hexagona* was noted as occurring abundantly in the F_{2g}, F_{2h}, and F_{2i} levels of the Dinant Basin; in the F_{2II} and the F_{2III} of the Namur Basin, and in the F_{II} beds of the Inlier of Theux.

HEXAGONARIA QUADRIGEMINA (Goldfuss)

Figures 3,*1a-e*; 8,2

Cyathophyllum quadrigeminum GOLDFUSS, 1826, p. 59, pl. 19, fig. 1a.

Prismatophyllum quadrigeminum SMITH, 1945, p. 46, pl. 14, fig. 5a,b.

Hexagonaria quadrigemina GLINSKA, 1955, p. 80, pl. 1, fig. 5.

Diagnosis.—Thick-walled *Hexagonaria* with large number of attenuate septa, complete tabulae, and characteristic quadripartite budding.

Lectotype.—STANLEY SMITH (1945, p. 46, pl. 14, fig. 5a,b) discuussed and figured a specimen illustrated by GOLDFUSS in 1826 (pl. 19, fig. 1b). The specimen was described by SMITH as having 40 septa, with the largest corallites about 10 mm. in total diameter, carinae feebly developed, and flat axial tabulae surrounded by small, inclined periaxial tabulae. I would regard this specimen as lectotype, and add the following to the description given SMITH. Corallite walls typically disphyllid in transverse section, with well-developed epitheca present as dark, amorphous calcite between prismatic layers of the respective corallites. The path shown by the walls is straight where septa are in opposition, but has commonly a weakly zigzag path where septa are in an offset position (uncommon for the species). Septa attenuate, thickest at intercorallite walls, thinning progressively to axial area with no dilation at border of the tabularium. Excellent quadripartite budding is shown by one corallite (SMITH, 1945, pl. 14, fig. 5a). The number of septa in the lectotype ranges from 34 to 46 and diameter of tabularium from 4 to 5 mm.

In longitudinal section the lectotype shows very well the characteristic complete, flat-topped tabulae. Septal fine structure is typical for the genus, with trabeculae making an angle of 30° to 40° with the epitheca and 45° to 55° with the margin of the tabularium.

Remarks.—SMITH noted that "feebly developed carinae are discernible" in the syntype (1945, p. 46) but none were noted by me. He also stated uncertainty as to whether this specimen is conspecific with the other syntypes, (op. cit., p. 46) and remarked that another should be chosen as lectotype. In my opinion, this specimen and thin sections of it display the most essential characteristics of the species, including quadripartite budding, and should be regarded as lectotype.

Description.—In nine colonies of *H. quadrigemina*, 138 corallites have a grand mean value of 39.3 for septa *(n)* and 4.9 mm. for *Dt.* The means of the coralla range from 34.3 to 43.9 for *n* and from 3.7 to 7.9 mm. for *Dt.* The total observed range in the 138 corallites is 32 to 48 for *n* and 3.2 to 9.5 mm. for *Dt* (Fig. 19).

Larger individuals (5-8 mm. *Dt*) with higher numbers of septa (*n* of 40-48) are most typical of the species (Fig. 3,*1c*), but numerous specimens were noted with all other distinguishing characteristics of the species, but smaller septal numbers and tabularia (Fig. 3,*1d*). Septa are attenuate, lacking dilation in the inner dissepimentarium,

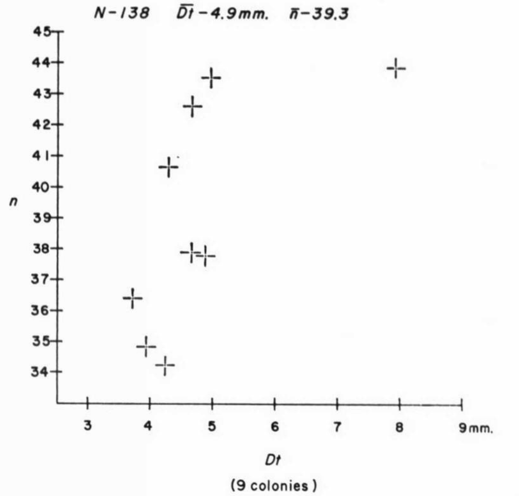


FIG. 19. *Hexagonaria quadrigemina.* Scatter diagram of mean number *(n)* of septa × diameter of tabularium *(Dt)* for each of 9 colonies. $\overline{Dt}$ and $\overline{n}$ are grand mean values for the total number *(N)* of corallites involved.

and first-order septa extend almost to the axis of the corallites where they may bend around the axis. Second-order septa are short, either failing to extend through the dissepimentarium or terminating at the border of the tabularium. The septa are not carinate.

The epithecal walls in *Hexagonaria quadrigemina* are massive and generally straight. The prismatic calcite layers of the corallite walls are clearly seen to be formed by the septal bases and lateral extensions of these bases. Septa are commonly in the opposition position on the two sides of the epitheca, adding to the straightness of the walls.

The dissepimentaria vary in width, although generally each approaches one-third of the corallite width in mature specimens. In immature forms, dissepimentaria may be very narrow or lacking. Dissepimentaria are generally composed of rows of 7 to 9 globular dissepiments, generally decreasing in size and inclining inward as the border of the tabularium is approached (Fig. 3, *1b*). At the inner margin of the dissepimentarium, the dissepiments are strongly inclined axially.

The tabularium within this species is marked by the presence of long, flat, complete tabulae, generally only weakly arched at the extreme, with lateral tabellae commonly present at some levels (Fig. 3,*1b*).

Septal fine structure is typical for the genus, with septal trabeculae making angles ranging from 30° to 55° with the epitheca, and angles of from 65° to 85° with the border of the tabularium.

As the trivial name of the species notes, *Hexagonaria quadrigemina* is characterized by parricidal budding resulting in four daughter corallites rising out of the parent corallite (Fig. 3,*1c*, left margin). This form of budding occurs commonly, but not exclusively, as intramural budding is also present and similar in type to that noted in other species of the genus.

Remarks.—The presence of subspecies within the *Hexagonaria quadrigemina* fauna of Belgium is a distinct possibility. Two types are found, a larger form with large numbers of septa and a smaller form with fewer septa. At present I do not think that sufficient data are available to support erection of a new subspecies.

Distribution.—*Hexagonaria quadrigemina* was noted as occurring in the Gi_b, Gi_c, and Gi_d rocks of the Dinant Basin; and in the Gi_{II} and Gi_{III} levels of the Namur Basin.

HEXAGONARIA DAVIDSONI (Milne-Edwards & Haime)

Figure 7,*1a,b*

Acervularia davidsoni Milne-Edwards & Haime, 1851, p. 418, pl. 9, fig. 4, 4a, 4b.

Diagnosis.—Species of *Hexagonaria* with median number of septa 40 to 42, septa generally attenuate, with septal dilation poorly marked and reaching to axis. Tabularium filled with long, irregularly placed tabulae interrupted by long septa.

Description.—In the one colony available for study (Fig. 7,*1a,b*), the species shows a mean septal number *(n)* of 42 and mean diameter *(Dt)* of 3.9 mm. The range within 15 corallites is 36 to 44 septa and 3.2 to 5.4 mm. *Dt.* The septa are uniformly long, and generally attenuate, with slight dilation present in a few corallites (Fig. 7,*1a*). First-order septa reach to axis, where a few join, but most are deflected, whereas second-order septa do not reach into tabularium. Epithecal walls are straight where septa are in opposition, but zigzag where septa are offset with respect to those of neighboring corallites.

The dissepimentarium is generally less than one-third of the total diameter of the corallites and is made up of rather steeply sloping rows of long, flat dissepiments, aligned at a very steep angle next to the tabularium (Fig. 7,*1b*). The tabularium contains long, irregularly sagging or sloping tabulae, which are most commonly intersected by long septa, with many accessory tabellae between septa.

The septal fine structure was not well displayed in the one longitudinal thin section available to me. However, all other species of *Hexagonaria* show septal trabeculae as perpendicular to the line of the row of dissepiments. In this case, septal trabeculae would make a large angle with the tabularium, possibly 70° to 80° and also a large angle with the epithecal wall, approximately 40° to 50°, thus conforming to the fine structure characteristic of the genus but differing from most species by the high angle made by the septal trabeculae and the epitheca.

Remarks.—This description is based on one colony that varies somewhat from the type (no. 105, Musée d'Histoire Naturelle de Paris) in that 1) walls are not as straight, 2) number of septa uniformly high in Belgian form, but not in the type specimen, and 3) the axial portion of the corallites contains fewer complete tabulae. These variations are not considered of specific value.

Distribution.—This species was represented by a single specimen in the Musée Royale d'Histoire Naturelle in Brussels (no. 16433). The specimen comes from the Frasnian (F_{2IIc}) of the Namur Basin.

HEXAGONARIA PHILOMENA Glinski

Figure 7,*2a,b*

Hexagonaria philomena Glinski, 1955, p. 98, pl. 2, fig. 1a,b.

Diagnosis.—"A species of *Hexagonaria* with the following special features: the septa pull in short [epithecal] septal strips; the tabulae are differentiated into flat major tabulae and convex side plates. A small inner wall is frequently present" (Glinski, 1955, p. 98).

Description.—Twenty corallites in the one available specimen of *Hexagonaria philomena* range from 32 to 36 *n* (total number of septa) and 3.8 to 6.0 mm. for *Dt* (diameter of tabularium). The mean values for these corallites are 33 *n* and 4.8 mm. *Dt.*

The septa are attenuate, being thickest at the point of insertion in the epithecal wall, not dilated, and extended to axis of the corallite, although they do not join (Fig. 7,*2a*). A majority of the corallites figured by Glinski show an open axial area and shorter septa than in the Belgian form. The walls have an undulating path, with septa in offset position, and marked by an infolding of epithecal calcite, which extends into the septa a short way. The dissepiments shown in transverse section are large and few in number.

The longitudinal section shows large, complete, flat-domed tabulae, and convex side tabellae, with no tendency toward development of axial and periaxial tabulae (Fig. 7,*2b*). The dissepimentarium is characterized by the presence of very large swollen dissepiments, few in numbers of rows, along with smaller, more numerous dissepiments seen at several levels within the corallites. Septal trabeculae are tilted inward and appear to form an angle of approximately 30° with the epitheca, and are progressively more inclined inward, reaching a maximum of approximately 45° at the border of the tabularium.

Remarks.—The above description is based on a single specimen which closely resembles the holotype (no. 25-514, Senckenbergisches Museum, Frankfurt) except that the septa in mature corallites are longer in the Belgian form, and no secondary calcite is present in the area surrounding the tabularium, as in the holotype. The species resembles *Hexagonaria davidsoni,* from which it can be differentiated by its fewer septa and completeness of tabulae.

Distribution.—Hexagonaria philomena is represented by thin sections (no. 16364) of one colony in the Musée Royale d'Histoire Naturelle in Brussels. The specimen was collected from Frasnian F_{2IIb} beds in the Namur Basin.

HEXAGONARIA HYPOCRATERIFORMIS (Goldfuss)

Figure 7,*3*

Cyathophyllum hypocrateriforme GOLDFUSS, 1826, p. 57, pl. 17, fig. 1c.

Diagnosis.—Large *Hexagonaria* with numerous attenuate septa, very large diameter of tabularium, and characteristic rows of peripheral buds.

Description.—In one transverse section available for study (Fig. 7,*3*), *Hexagonaria hypocrateriformis* displays 50.1 septa and 6.5 mm. *Dt* as mean values for 6 mature corallites. The total observed range in these individuals is 48 to 52 septa *(n)* and 5.2 to 8.2 mm. diameter of tabularium *(Dt)*. The septa are attenuate, thickest at the epithecal wall, and first-order septa reach approximately 0.75 of the way to the axis, leaving a large open axial area. Second-order septa do not extend into the tabularium. The epithecal walls are thick, straight or evenly curved, with broad-based septa adding to the massive appearance of the walls. As shown by GOLDFUSS (1826, pl. 17), the species is characterized by the form of budding, in which the young tend to form rows of two or three individuals along one side of the parent. In the figured transverse section, several generations of such buds can be noted around the large corallite in the center of the photograph.

Remarks.—The description of this single thin section is included for completeness of the fauna. The species would be expected to occur commonly in Givetian rocks of Belgium, but none were collected in the field.

Distribution.—The one specimen available for study was collected in the Givetian *(Gi_b)* of the Dinant Basin.

HEXAGONARIA DARWINI (Frech)

Figure 11,*2a,b*

Cyathophyllum darwini FRECH, 1885, p. 36, not figured; ——FRECH, 1886, p. 73, pl. E ,fig. 2,2a.

Peneckiella darwini SOSHKINA, 1939, p. 26, pl. 8, fig. 70-71;——SOSHKINA, 1951, p. 107, pl. 20, fig. 1.

Diagnosis.—Species of *Hexagonaria* characterized by large number of short septa, with first-order septa extending only a short way into tabularium and second-order septa appearing as short stubs or extending one-half way through dissepimentarium. Broad open tabularium filled with bowl-shaped largely complete tabulae, while narrow dissepimentarium is occupied by few rows of broad flat dissepiments.

Description.—Only one colony was found, with 6 corallites yielding mean values of 38.8 for *n* and 3.8 mm. for *Dt*. The total observed range was 37 to 42 septa *(n)* and 3.3 to 4.0 mm. *Dt*.

In transverse section the feature most characteristic of this species is seen as short undilated septa. The first-order septa extend only a short way into the tabularium, whereas second-order septa are only approximately half as long, and reach only part way through the dissepimentarium, usually approximately half way (Fig. 11,*2a*). The epithecal walls are straight and septa are ordinarily more or less in opposition to those of neighboring corallites.

In longitudinal section are seen characteristics that make the species easily differentiated from others noted in this study. The tabularium is characterized by the presence of long, flat-bottomed, bowl-shaped tabulae, noted in section as bending up at the lateral margins of the tabularium (Fig. 11,*2b*). The dissepiments are generally flattened and form rows of a few dissepiments which slope progressively inward, reaching the slope of the walls of the tabularium. At several levels, the dissepimentarium is seen to be composed of only one (or two) very large, flat dissepiments which appear to be almost continuous into tabulae.

Septal fine structures are typical for the genus, with maximum inclination of septal trabeculae noted at the border of the tabularium, reaching angles measured at 53° to 66° from vertical.

Remarks.—The above description is based on thin sections of a single colony in the Musée Royale d'Histoire Naturelle de Bruxelles (no. 16713). It agrees in all respects with the species as described by FRECH. The form figured by SOSHKINA is most probably conspecific, but no longitudinal section was figured by that author.

Distribution.—The specimen studied was collected in Frasnian (*F_{2III}*) beds of the Namur Basin.

HEXAGONARIA ROHRENSIS Glinski

Figure 11,*3a,b*

Hexagonaria rohrensis GLINSKI, 1955, p. 93, pl. 1, fig. 1a,b.

Diagnosis.—Species of *Hexagonaria* with shortened, attenuate septa, and paucity of dissepiments.

Description.—In the one colony of *Hexagonaria rohrensis* collected, 20 corallites yield mean values of 30.6 for *n* and 4.3 mm. for *Dt*. The observed range is 28 to 34 septa and 3.0 to 5.4 mm. for diameter *(Dt)*.

In transverse section, 3 or 4 rows of dissepiments are the maximum observed, and it is not uncommon to find corallites totally lacking in development of dissepiments, at least on one side through a part of their growth. The septa are attenuate, thickest at the point of their insertion into the epitheca, and only reach 0.7 of the way into the calyx (Fig. 11,*3a*). The resultant broad tabularium contains flat or slightly flat-topped domal tabulae that are widely spaced and generally whole. The dissepimentarium is restricted to 3 or 4 rows of dissepiments (Fig. 11,*3b*).

Distribution.—The species was only collected from Givetian (*Gi_b*) rocks of the southern Dinant Basin (Couvin).

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